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LUDWIG AND MODERN PHYSIOLOGY.[1]

I. INTRODUCTION.

THE death of any discoverer—of any one who has added largely to the sum of human knowledge—affords a reason for inquiring what his work was and how he accomplished it. This inquiry has interest even when the work has been completed in a few years and has been limited to a single line of investigation—much more when the life has been associated with the origin and development of a new science and has extended over half a century.

The Science of Physiology as we know it came into existence fifty years ago with the beginning of the active life of Ludwig, in the same sense that the other great branch of Biology, the Science of Living Beings (Ontology), as we now know it, came into existence with the appearance of the "Origin of Species". In the order of time Physiology had the advantage, for the new Physiology was accepted some ten years before the Darwinian epoch. Notwithstanding, the content of the science is relatively so unfamiliar, that before entering on the discussion of the life and work of the man who, as I shall endeavour to show, had a larger share in founding it than any of his contemporaries, it is necessary to define its limits and its relations to other branches of knowledge.

[1] Founded upon a lecture delivered at the Royal Institution, Jan. 24, 1896.

The word Physiology has in modern times changed its meaning. It once comprehended the whole knowledge of Nature. Now it is the name for one of the two Divisions of the Science of Life. In the progress of investigation the study of that Science has inevitably divided itself into two: *Ontology*, the Science of Living Beings; *Physiology*, the Science of Living Processes, and thus, inasmuch as Life consist in processes, of Life itself. Both strive to understand the complicated relations and endless varieties which present themselves in living Nature, but by different methods. Both refer to general principles, but they are of a different nature.

To the *Ontologist*, the student of Living Beings, Plants or Animals, the great fact of Evolution, namely, that from the simplest beginning our own organism, no less than that of every animal and plant with its infinite complication of parts and powers, unfolds the plan of its existence—taken with the observation that that small beginning was, in all excepting the lowest forms, itself derived from two parents, equally from each—is the basis from which his study and knowledge of the world of living beings takes its departure. For on these two facts—Evolution and Descent—the explorer of the forms, distribution and habits of animals and plants has, since the Darwinian epoch, relied with an ever-increasing certainty, and has found in them the explanation of every phenomenon, the solution of every problem relating to the subject of his inquiry. Nor could he wish for a more secure basis. Whatever doubts or misgivings exist in the minds of "non-biologists" in relation to it, may be attributed partly to the association with the doctrine of Evolution of questions which the true naturalist regards as transcendental; partly to the perversion or weakening of meaning which the term has suffered in consequence of its introduction into the language of common life, and particularly to the habit of applying it to any kind of progress or improvement, anything which from small beginnings *gradually* increases. But, provided that we limit the term to its original sense—the Evolution of a living being from its germ by a *continuous*, not a gradual process—there is no

conception which is more free from doubt either as to its meaning or reality. It is inseparable from that of Life itself, which is but the *unfolding* of a predestined harmony, of a prearranged consensus and synergy of parts.

The other branch of Biology, that with which Ludwig's name is associated, deals with the same facts in a different way. While Ontology regards animals and plants as individuals and in relation to other individuals, Physiology considers the processes themselves of which life is a complex. This is the most obvious distinction, but it is subordinate to the fundamental one, namely, that while Ontology has for its basis laws which are in force only in its own province, those of Evolution, Descent, and Adaptation, we Physiologists, while accepting these as true, found nothing upon them, using them only for euristic purposes, *i.e.*, as guides to discovery, not for the purpose of explanation. Purposive Adaptation, for example, serves as a clue, by which we are constantly guided in our exploration of the tangled labyrinth of vital processes. But when it becomes our business to explain these processes—to say how they are brought about—we refer them not to biological principles of any kind, but to the Universal Laws of Nature. Hence it happens that with reference to each of these processes, our inquiry is rather how it occurs than why it occurs.

It has been well said that the Natural Sciences are the children of necessity. Just as the other Natural Sciences owed their origin to the necessity of acquiring that control over the forces of Nature without which life would scarcely be worth living, so Physiology arose out of human suffering and the necessity of relieving it. It sprang indeed out of Pathology. It was suffering that led us to know, as regards our own bodies, that we had internal as well as external organs, and probably one of the first generalisations which arose out of this knowledge was, that "if one member suffer all the members suffer with it"—that all work together for the good of the whole. In earlier times the *good* which was thus indicated was associated in men's minds with human welfare exclusively. But it was eventually seen that Nature has no less consideration for

the welfare of those of her products which to us seem hideous or mischievous, than for those which we regard as most useful to man or most deserving of his admiration. It thus became apparent that the good in question could not be human exclusively, but as regards each animal *its own good*—and that in the organised world the existence and life of every species is brought into subordination to one purpose—its own success in the struggle for existence.[1]

From what has preceded it may be readily understood that in Physiology, Adaptation takes a more prominent place than Evolution or Descent. In the prescientific period adaptation was everything. The observation that any structure or arrangement exhibited marks of adaptation to a useful purpose was accepted not merely as a guide in research, but as a full and final explanation. Of an organism or organ which perfectly fulfilled, in its structure and working, the end of its existence, nothing further required to be said or known. Physiologists of the present day recognise as fully as their predecessors that perfection of contrivance which displays itself in all living structures, the more exquisitely the more minutely they are examined. No one, for example, has written more emphatically on this point than did Ludwig. In one of his discourses, after showing how Nature exceeds the highest standard of human attainment—how she fashions as it were out of nothing and without tools, instruments of a perfection which the human artificer cannot reach, though provided with every suitable material—wood, brass, glass, india-rubber—he gives the organ of sight as a signal example, referring among its

[1] I am aware that in thus stating the relation between adaptation and the struggle for existence, I may seem to be reversing the order followed by Mr. Darwin, inasmuch as he regarded the survival of organisms which are fittest for their place in Nature, and of parts which are fittest for their place in the organism, as the agency by which adaptedness is brought about. However this may be expressed it cannot be doubted that fitness is an essential of organisms. Living beings are the only things in Nature which by virtue of evolution and descent are able to adapt themselves to their surroundings. It is therefore only so far as *organism* (with all its attributes) is presupposed, that the dependence of adaptation on survival is intelligible.

other perfections to the rapidity with which the eye can be fixed on numerous objects in succession and the instantaneous and unconscious estimates which we are able to form of the distances of objects, each estimate involving a process of arithmetic which no calculating machine could effect in the time.[1] In another discourse—that given at Leipzig when he entered on his professorship in 1865—he remarks that when in our researches into the finer mechanism of an organ we at last come to understand it, we are humbled by the recognition "that the human inventor is but a blunderer as compared with the unknown Master of the animal creation".[2]

Some readers will perhaps remember how one of the most brilliant of philosophical writers, in a discourse to the British Association delivered a quarter of a century ago, averred on the authority of a great Physiologist that the eye, regarded as an optical instrument, was so inferior a production that if it were the work of a mechanician it would be unsaleable. Without criticising or endeavouring to explain this paradox, I may refer to it as having given the countenance of a distinguished name to a misconception which I know exists in the minds of many persons, to the effect that the scientific Physiologist is more or less blind to the evidence of design in creation. On the contrary, the view taken by Ludwig, as expressed in the words I have quoted, is that of all Physiologists. The disuse of the teleological expressions which were formerly current does not imply that the indications of contrivance are less appreciated, for, on the contrary, we regard them as more characteristic of organism as it presents itself to our observation than any other of its endowments. But, if I may

[1] I summarise here from a very interesting lecture entitled "Leid und Freude in der Naturforschung" published in the *Gartenlaube* (Nos. 22 and 23) in 1870.

[2] The words translated in the above sentence are as follows: "Wenn uns endlich die Palme gereicht wird, wenn wir ein Organ in seinem Zuzammenhang begreifen, so wird unser stolzes Gattungsbewusstsein durch die Erkenntniss niedergedrückt, dass der menschlicher Erfinder ein Stümper gegen den unbekannten Meister der thierischen Schöpfung sei".

be permitted to repeat what has been already said, we use the evidences of adaptation differently. We found no explanation on this or any other biological principle, but refer all the phenomena by which these manifest themselves to the simpler and more certain Physical Laws of the Universe.

Why must we take this position? First, because it is a general rule in investigations of all kinds to explain the more complex by the more simple. The material Universe is manifestly divided into two parts, the living and the non-living. We may, if we like, take the living as our Norma, and say to the Physicists, You must come to us for Laws, you must account for the play of energies in universal nature by referring them to Evolution, Descent, Adaptation. Or we may take these words as true expressions of the mutual relations between the phenomena and processes peculiar to living beings, using for the explanation of the processes themselves the same methods which we should employ if we were engaged in the investigation of analogous processes going on independently of life. Between these two courses there seems to me to be no third alternative, unless we suppose that there are two material Universes, one to which the material of our bodies belongs, the other comprising everything that is not either plant or animal.

The second reason is a practical one. We should have to go back to the time which I have ventured to call pre-scientific, when the world of life and organisation was supposed to be governed exclusively by its own Laws. The work of the past fifty years has been done on the opposite principle, and has brought light and clearness where there was before obscurity and confusion. All this progress we should have to repudiate, but this would not be all. We should have to forego the prospect of future advance. Whereas by holding on our present course, gradually proceeding from the more simple to the more complex, from the physical to the vital, we may confidently look forward to extending our knowledge considerably beyond its present limits.

A no less brilliant writer than the one already referred to, who is also no longer with us, asserted that mind was a

secretion of the brain in the same sense that bile is a secretion of the liver or urine that of the kidney; and many people have imagined this to be the necessary outcome of a too mechanical way of looking at vital phenomena, and that Physiologists, by a habit of adhering strictly to their own method, have failed to see that the organism presents problems to which this method is not applicable, such, *e.g.*, as the origin of the organism itself, or the origin and development in it of the mental faculty. The answer to this suggestion is that these questions are approached by Physiologists only in so far as they are approachable. We are well aware that our business is with the unknown knowable, not with the transcendental. During the last twenty years there has been a considerable forward movement in Physiology in the psychological direction, partly dependent on discoveries as to the localisation of the higher functions of the nervous system, partly on the application of methods of measurement to the concomitant phenomena of psychical processes. And these researches have brought us to the very edge of a region which cannot be explored by our methods—where measurements of time or of space are no longer possible.

In approaching this limit the Physiologist is liable to fall into two mistakes—on the one hand, that of passing into the transcendental without knowing it; on the other, that of assuming that what he does not know is not knowledge. The first of these risks seems to me of little moment; first, because the limits of natural knowledge in the psychological direction have been well defined by the best writers, as, *e.g.*, by du Bois-Reymond in his well-known essay "On the Limits of Natural Knowledge," but chiefly because the investigator who knows what he is about is arrested *in limine* by the impossibility of applying the experimental method to questions beyond its scope. The other mistake is chiefly fallen into by careless thinkers, who, while they object to the employment of intuition even in regions where intuition is the only method by which anything can be learned, attempt to describe and define mental processes in mechanical terms, assigning to these terms meanings which science

does not recognise, and thus slide into a kind of speculation which is as futile as it is unphilosophical.

II. LUDWIG AS INVESTIGATOR AND TEACHER.

The uneventful history of Ludwig's life—how early he began his investigation of the anatomy and function of the kidneys; how he became just fifty years ago titular Professor at Marburg, in the small University of his native State, Hesse Cassel; how in 1849 he removed to Zürich as actual Professor and thereupon married; how he was six years later promoted to Vienna—has already been admirably related in these pages by Dr. Stirling. In 1865, after twenty years of professorial experience, but still in the prime of life and, as it turned out, with thirty years of activity still before him, he accepted the Chair of Physiology at Leipzig. His invitation to that great University was by far the most important occurrence in his life, for the liberality of the Saxon Government, and particularly the energetic support which he received from the enlightened Minister v. Falkenstein, enabled him to accomplish for Physiology what had never before been attempted on an adequate scale. No sooner had he been appointed than he set himself to create what was essential to the progress of the Science—a great Observatory, arranged not as a Museum, but much more like a physical and chemical Laboratory, provided with all that was needed for the application of exact methods of research to the investigation of the processes of Life. The idea which he had ever in view, and which he carried into effect during the last thirty years of his life with signal success, was to unite his life-work as an investigator with the highest kind of teaching. Even at Marburg and at Zürich he had begun to form a *School;* for already men nearly of his own age had rallied round him. Attracted in the first instance by his early discoveries, they were held by the force of his character, and became permanently associated with him in his work as his loyal friends and followers—in the highest sense his *scholars.* If, therefore, we speak of Ludwig as one of the

greatest *teachers* of Science the world has seen, we have in mind his relation to the men who ranged themselves under his leadership in the building up of the Science of Physiology, without reference to his function as an ordinary academical teacher.

Of this relation we can best judge by the careful perusal of the numerous biographical memoirs which have appeared since his death, more particularly those of Professor His [1] (Leipzig), of Professor Kronecker [2] (Bern), who was for many years his coadjutor in the Institute, of Professor v. Fick [3] (Würzburg), of Professor v. Kries [4] (Freiburg), of Professor Mosso [5] (Turin), of Professor Fano [6] (Florence), of Professor Tigerstedt [7] (Upsala), of Professor Stirling [8] in England. With the exception of Fick, whose relations with Ludwig were of an earlier date, and of his colleague in the Chair of Anatomy, all of these distinguished teachers were at one time workers in the Leipzig Institute. All testify their love and veneration for the master, and each contributes some striking touches to the picture of his character.

All Ludwig's investigations were carried out with his scholars. He possessed a wonderful faculty of setting each man to work at a problem suited to his talent and previous training, and this he carried into effect by associating him with himself in some research which he had either in progress or in view. During the early years of the Leipzig period, all the work done under his direction was published in the well-known volumes of the *Arbeiten*, and

[1] His. "Karl Ludwig und Karl Thiersch." *Akademische Gedächtnissrede*, Leipzig, 1895.

[2] Kronecker. "Carl Friedrich Wilhelm Ludwig." *Berliner Klin. Wochensch.*, 1895, No. 21.

[3] A. Fick. "Karl Ludwig." Nachruf. *Biographische Blätter*, Berlin, vol. i., pt. 3.

[4] v. Kries. "Carl Ludwig." Freiburg, Bd. i., 1895.

[5] Mosso. "Karl Ludwig." *Die Nation*, Berlin, Nos. 38, 39.

[6] Fano. "Per Carlo Ludwig Commemorazione." *Clinica Moderna*, Florence, i., No. 7.

[7] Tigerstedt. "Karl Ludwig." Denkrede. *Biographische Blätter*, Berlin, vol. i., pt. 3.

[8] Stirling. "SCIENCE PROGRESS," vol. iv., No. 21.

subsequently in the *Archiv fur Anat. und Physiologie* of du Bois-Reymond. Each "Arbeit" of the laboratory appeared in print under the name of the scholar who operated with his master in its production, but the scholar's part in the work done varied according to its nature and his ability. Sometimes, as v. Kries says, he sat on the window-sill while Ludwig with the efficient help of his laboratory assistant Salvenmoser, did the whole of the work. In all cases Ludwig not only formulated the problem, but indicated the course to be followed in each step of the investigation, calling the worker, of course, into counsel. In the final working up of the results he always took a principal part, and often wrote the whole paper. But whether he did little or much, he handed over the whole credit of the performance to his coadjutor. This method of publication has no doubt the disadvantage that it leaves it uncertain what part each had taken; but it is to be remembered that this drawback is unavoidable whenever master and scholar work together, and is outweighed by the many advantages which arise from this mode of co-operation. The instances in which any uncertainty can exist in relation to the real authorship of the Leipzig work are exceptional. The well-informed reader does not need to be told that Mosso or Schmidt, Brunton or Gaskell, Stirling or Wooldridge were the authors of their papers in a sense very different from that in which the term could be applied to some others of Ludwig's pupils. On the whole the plan must be judged of by the results. It was by working with his scholars that Ludwig trained them to work afterwards by themselves; and thereby accomplished so much more than other great teachers have done.

I do not think that any of Ludwig's contemporaries could be compared to him in respect of the wide range of his researches. In a science distinguished from others by the variety of its aims, he was equally at home in all branches, and was equally master of all methods, for he recognised that the most profound biological question can only be solved by combining anatomical, physical and and chemical inquiries. It was this consideration which led

him in planning the Leipzig Institute to divide it into three parts, experimental (in the more restricted sense), chemical and histological. Well aware that it was impossible for a man who is otherwise occupied to maintain his familiarity with the technical details of Histology and Physiological Chemistry, he placed these departments under the charge of younger men capable of keeping them up to the rapidly advancing standard of the time, his relations with his coadjutors being such that he had no difficulty in retaining his hold of the threads of the investigation to which these special lines of inquiry were contributory.

It is scarcely necessary to say that as an experimenter Ludwig was unapproachable. The skill with which he carried out difficult and complicated operations, the care with which he worked, his quickness of eye and certainty of hand were qualities which he had in common with great surgeons. In employing animals for experiment he strongly objected to rough and ready methods, comparing them to "firing a pistol into a clock to see how it works". Every experiment ought, he said, to be carefully planned and meditated on beforehand, so as to accomplish its scientific purpose and avoid the infliction of pain. To ensure this he performed all operations himself, only rarely committing the work to a skilled coadjutor.

His skill in anatomical work was equally remarkable. It had been acquired in early days, and appeared throughout his life to have given him very great pleasure, for Mosso tells how, when occupying the room adjoining that in which Ludwig was working as he usually did by himself, he heard the outbursts of glee which accompanied each successful step in some difficult anatomical investigation.

Let us now examine more fully the part which Ludwig played in the revolution of ideas as to the nature of vital processes which, as we have seen, took place in the middle of the present century.

Although, as we shall see afterwards, there were many men who, before Ludwig's time, investigated the phenomena of life from the physical side, it was he and the contemporaries who were associated with him who first clearly

recognised the importance of the principle that vital phenomena *can only be understood by comparison with their physical counterparts*, and foresaw that in this principle the future of Physiology was contained as in a nutshell. Feeling strongly the fruitlessness and unscientific character of the doctrines which were then current, they were eager to discover chemical and physical relations in the processes of life. In Ludwig's intellectual character this eagerness expressed his dominant motive. Notwithstanding that his own researches had in many instances proved that there are important functions and processes in the animal organism which have no physical or chemical analogues, he never swerved either from the principle or from the method founded upon it.

Although Ludwig was strongly influenced by the rapid progress which was being made in scientific discovery at the time that he entered on his career, he derived little from his immediate predecessors in his own science. He is sometimes placed among the pupils of the great Comparative Anatomist and Physiologist, J. Müller. This, however, is a manifest mistake, for Ludwig did not visit Berlin until 1847, when Müller was nearly at the end of his career. At that time he had already published researches of the highest value (those on the Mechanism of the Circulation and on the Physiology of the Kidney), and had set forth the line in which he intended to direct his investigations. The only earlier Physiologist with whose work that of Ludwig can be said to be in real continuity was E. H. Weber, whom he succeeded at Leipzig, and strikingly resembled in his way of working. For Weber, Ludwig expressed his veneration more unreservedly than for any other man, excepting perhaps Helmholtz, regarding his researches as the foundation on which he himself desired to build. Of his colleagues at Marburg he was indebted in the first place to the anatomist, Professor Ludwig Fick, in whose department he began his career as Prosector, and to whom he owed facilities without which he could not have carried out his earlier researches; and in an even higher degree to the great chemist, R. W. Bunsen, from whom he derived that training in the exact

sciences which was to be of such inestimable value to him afterwards.

There is reason, however, to believe that, as so often happens, Ludwig's scientific progress was much more influenced by his contemporaries than by his seniors. In 1847, as we learn on the one hand from du Bois-Reymond, on the other from Ludwig himself, he visited Berlin for the first time. This visit was an important one both for himself and for the future of Science, for he there met three men of his own age, Helmholtz, du Bois-Reymond and Brücke, who were destined to become his life-friends, all of whom lived nearly as long as Ludwig himself, and attained to the highest distinction. They all were full of the same enthusiasm. As Ludwig said when speaking of this visit: "We four imagined that we should constitute Physiology on a chemico-physical foundation, and give it equal scientific rank with Physics, but the task turned out to be much more difficult than we anticipated". These three young men, who were devoted disciples of the great Anatomist, had the advantage over their master in the better insight which their training had given them into the fundamental principles of scientific research. They had already gathered around themselves a so-called "physical" school of Physiology, and welcomed Ludwig on his arrival from Marburg as one who had of his own initiative undertaken in his own University *das Befreiungswerk aus dem Vitalismus.*

The determination to refer all vital phenomena to their physical or chemical counterparts or analogues, which, as I have said, was the dominant motive in Ludwig's character, was combined with another quality of mind which if not equally influential was even more obviously displayed in his mode of thinking and working. His first aim, even before he sought for any explanation of a structure or of a process, was to possess himself, by all means of observation at his disposal, of a complete objective conception of all its relations. He regarded the faculty of vivid sensual realisation (*lebendige sinnliche Anschauung*) as of special value to the investigator of natural phenomena, and did his best to cultivate it in those who worked with him in the

laboratory. In himself, this *objective* tendency (if I may be permitted the use of a word which, if not correct, seems to express what I mean) might be regarded as almost a defect, for it made him indisposed to appreciate any sort of knowledge which deals with the abstract. He had a disinclination to philosophical speculation which almost amounted to aversion, and, perhaps for a similar reason, avoided the use of mathematical methods even in the discussion of scientific questions which admitted of being treated mathematically—contrasting in this respect with his friend du Bois-Reymond, resembling Brücke. But as a teacher the quality was of immense use to him. His power of vivid realisation was the *substratum* of that many-sidedness which made him, irrespectively of his scientific attainments, so attractive a personality.

I am not sure that it can be generally stated that a keen scientific observer is able to appreciate the artistic aspects of Nature. In Ludwig's case, however, there is reason to think that æsthetic faculty was as developed as the power of scientific insight. He was a skilful draughtsman but not a musician; both arts were, however, a source of enjoyment to him. He was a regular frequenter of the *Gewandhaus* concerts, and it was his greatest pleasure to bring together gifted musicians in his house, where he played the part of an intelligent and appreciative listener. Of painting he knew more than of music, and was a connoisseur whose opinion carried weight. It is related that he was so worried by what he considered bad art, that after the redecoration of the *Gewandhaus* concert-room, he was for some time deprived of his accustomed pleasure in listening to music.

Ludwig's social characteristics can only be touched on here in so far as they serve to make intelligible his wonderful influence as a teacher. Many of his pupils at Leipzig have referred to the *schöne Gemeinsamkeit* which characterised the life there. The harmonious relation which, as a rule, subsisted between men of different education and different nationalities, could not have been maintained had not Ludwig possessed side by side with that inflexible earnestness which he showed in all matters of work or

duty a certain youthfulness of disposition which made it possible for men much younger than himself to accept his friendship. This sympathetic geniality was, however, not the only or even the chief reason why Ludwig's pupils were the better for having known him. There were not a few of them who for the first time in their lives came into personal relation with a man who was utterly free from selfish aims and vain ambitions, who was scrupulously conscientious in all that he said and did, who was what he seemed, and seemed what he was, and who had no other aim than the advancement of his science, and in that advancement saw no other end than the increase of human happiness. These qualities displayed themselves in Ludwig's daily active life in the laboratory, where he was to be found whenever work of special interest was going on; but still more when, as happened on Sunday-mornings, he was "at home" in the library of the Institute—the corner room in which he ordinarily worked. Many of his "scholars" have put on record their recollections of these occasions, the cordiality of the master's welcome, the wide range and varied interest of his conversation, and the ready appreciation with which he seized on anything that was new or original in the suggestions of those present. Few men live as he did, "*im Gaznen, Guten, Schönen,*" and of those still fewer know how to communicate out of their fulness to others.

III. THE OLD AND THE NEW VITALISM.

Since the middle of the century the progress of Physiology has been continuous. Each year has had its record, and has brought with it new accessions to knowledge. In one respect the rate of progress was more rapid at first than it is now, for in an unexplored country discovery is relatively easy. In another sense it was slower, for there are now scores of investigators for every one that could be counted in 1840 or 1850. Until recently there has been throughout this period no tendency to revert to the old methods—no new departure—no divergence from the principles which Ludwig did so much to enforce and exemplify.

The wonderful revolution which the appearance of the *Origin of Species* produced in the other branch of Biology, promoted the progress of Physiology, by the new interest which it gave to the study, not only of structure and development, but of all other vital phenomena. It did not, however, in any sensible degree affect our *method* or alter the direction in which Physiologists had been working for two decades. Its most obvious effect was to sever the two subjects from each other. To the Darwinian epoch Comparative Anatomy and Physiology were united, but as the new Ontology grew, it became evident that each had its own problems and its own methods of dealing with them.

The old vitalism of the first half of the century is easily explained. It was generally believed that, on the whole, things went on in the living body as they do outside of it, but when a difficulty arose in so explaining them the Physiologist was ready at once to call in the aid of a "*vital force*". It must not, however, be forgotten that, as I have already indicated, there were great teachers (such, for example, as Sharpey and Allen Thomson in England, Magendie in France, Weber in Germany) who discarded all vitalistic theories, and concerned themselves only with the study of the time- and place-relations of phenomena; men who were before their time in insight, and were only hindered in their application of chemical and physical principles to the interpretation of the processes of life by the circumstance that chemical and physical knowledge was in itself too little advanced. Comparison was impossible, for the standards were not forthcoming.

Vitalism in its original form gave way to the rapid advance of knowledge as to the correlation of the physical sciences which took place in the forties. Of the many writers and thinkers who contributed to that result, J. R. Mayer and Helmholtz did so most directly, for the contribution of the former to the establishment of the Doctrine of the Conservation of Energy had physiological considerations for its point of departure; and Helmholtz, at the time he wrote the *Erhaltung der Kraft*, was still a Physiologist. Consequently when Ludwig's celebrated *Lehrbuch*

came out in 1852, the book which gave the *coup de grâce* to vitalism in the old sense of the word, his method of setting forth the relations of vital phenomena by comparison with their physical or chemical counterparts, and his assertion that it was the task of Physiology to make out their necessary dependence on elementary conditions, although in violent contrast with current doctrine, were in no way surprising to those who were acquainted with the then recent progress of research. Ludwig's teaching was indeed no more than a general application of principles which had already been applied in particular instances.

The proof of the non-existence of a special "vital force" lies in the demonstration of the adequacy of the known sources of energy in the organism to account for the actual day by day expenditure of heat and work—in other words, on the possibility of setting forth an energy balance sheet in which the quantity of food which enters the body in a given period (hour or day) is balanced by an exactly corresponding amount of heat produced or external work done. It is interesting to remember that the work necessary for preparing such a balance sheet (which Mayer had attempted, but, from want of sufficient data, failed in) was begun thirty years ago in the laboratory of the Royal Institution by the Foreign Secretary of the Royal Society. But the determinations made by Dr. Frankland related to one side of the balance sheet, that of income. By his researches in 1866 he gave Physiologists for the first time reliable information as to the heat value (*i.e.*, the amount of heat yielded by the combustion) of different constituents of food. It still remained to apply methods of exact measurement to the expenditure side of the account. Helmholtz had estimated this, as regards man, as best he might, but the technical difficulties of measuring the expenditure of heat of the animal body appeared until lately to be almost insuperable. Now that it has been at last successfully accomplished, we have the experimental proof that in the process of life there is no production or disappearance of energy. It may be said that it was unnecessary to prove what no scientifically sane man doubted. There are, however, reasons why it is

of importance to have objective evidence that food is the sole and adequate source of the energy which we day by day or hour by hour disengage, whether in the form of heat or external work.

In the opening paragraph of this section it was observed that *until recently* there had been no tendency to revive the vitalistic notion of two generations ago. In introducing the words in italics I referred to the existence at the present time in Germany of a sort of reaction, which under the term "Neovitalismus" has attracted some attention—so much indeed that at the *Versammlung Deutscher Naturforscher* at Lübeck last September, it was the subject of one of the general addresses. The author of this address, Prof. Rindfleisch, was, I believe, the inventor of the word; but the origin of the movement is usually traced to a work on Physiological Chemistry which an excellent translation by the late Dr. Wooldridge has made familiar to English students. The author of this work owes it to the language he employs in the introduction on "Mechanism and Vitalism," if his position has been misunderstood, for in that introduction he distinctly ranges himself on the vitalistic side. As, however, his vitalism is of such a kind as not to influence his method of dealing with actual problems, it is only in so far of consequence as it may affect the reader. For my own part I feel grateful to Professor Bange for having produced an interesting and readable book on a dry subject, even though that interest may be partly due to the introduction into the discussion of a question which, as he presents it, is more speculative than scientific.

As regards other physiological writers to whom vitalistic tendencies have been attributed, it is to be observed that none of them have even suggested that the doctrine of a "vital force" in its old sense should be revived. Their contention amounts to little more than this, that in certain recent instances improved methods of research appear to have shown that processes at first regarded as entirely physical or chemical do not conform so precisely as they were expected to do to chemical and physical laws. As these instances are all essentially analogous, reference to one will serve to explain the bearing of the rest.

Those who have any acquaintance with the structure of the animal body will know that there exists in the higher animals, in addition to the system of veins by which the blood is brought back from all parts to the heart, another less considerable system of branched tubes, the lymphatics, by which, if one may so express it, the leakage of the blood-vessels is collected. Now, without inquiring into the *why* of this system, Ludwig and his pupils made and continued for many years elaborate investigations which were for long the chief sources of our knowledge, their general result being that the efficient cause of the movement of the lymph, like that of the blood, was mechanical. At the Berlin Congress in 1890 new observations by Professor Heidenhain of Breslau made it appear that under certain conditions the process of lymph formation does not go on in strict accordance with the physical laws by which leakage through membranes is regulated, the experimental results being of so unequivocal a kind that, even had they not been confirmed, they must have been received without hesitation. How is such a case as this to be met? The "Neovitalists" answer promptly by reminding us that there are cells, *i.e.*, living individuals, placed at the inlets of the system of drainage without which it would not work, that these let in less or more liquid according to circumstances, and that in doing so they act in obedience, not to physical laws, but to vital ones—to internal laws which are special to themselves.

Now, it is perfectly true that living cells, like working bees, are both the architects of the hive and the sources of its activity, but if we ask how honey is made it is no answer to say that the bees make it. We do not require to be told that cells have to do with the making of lymph as with every process in the animal organism, but what we want to know is *how* they work, and to this we shall never get an answer so long as we content ourselves with merely explaining one unknown thing by another. The action of cells must be explained, if at all, by the same method of comparison with physical or chemical analogues that we employ in the investigation of organs.

Since 1890 the problem of lymph formation has been

attacked by a number of able workers, among others here in London, by Dr. Starling of Guy's Hospital, who, by sedulously studying the conditions under which the discrepancies between the actual and the expected have arisen, has succeeded in untying several knots. In reference to the whole subject, it is to be noticed that the process by which difficulties are brought into view is the same as that by which they are eliminated. It is one and the same method throughout, by which step by step, knowledge perfects itself—at one time by discovering errors, at another by correcting them; and if at certain stages in this progress difficulties seem insuperable, we can gain nothing by calling in, even provisionally, the aid of any sort of *Eidolon*, whether "cell," "protoplasm" or internal principle.

It thus appears to be doubtful whether any of the biological writers who have recently professed vitalistic tendencies are in reality vitalists. The only exception that I know is to be found in the writings of a well-known morphologist, Dr. Hans Driesch,[1] who has been led by his researches on what is now called the Mechanics of Evolution to revert to the fundamental conception of vitalism, that the laws which govern vital processes are not physical, but biological—that is, peculiar to the living organism, and limited thereto in their operation. Dr. Driesch's researches as to the modifications which can be produced by mechanical interference in the early stages of the process of ontogenesis have enforced upon him considerations which he evidently regards as new, though they are familiar enough to Physiologists. He recognises that although by the observation of the successive stages in the ontogenetic process, one may arrive at a perfect knowledge of the relation of these stages to each other, this leaves the efficient causes of the development unexplained (*führt nicht zu einem Erkenntniss ihrer bewirkenden Ursachen*)—it does not teach us why one

[1] Driesch. "Entwicklungsmechanische Studien": a series of ten Papers, of which the first six appeared in the *Zeitsch. f. w. Zoologie*, vols. liii. and lv.; the rest in the *Mittheilungen* of the Naples Station.

form springs out of another. This brings him at once face to face with a momentous question. He has to encounter three possibilities — he may either join the camp of the biological agnostics and say with du Bois-Reymond, "*ignoramus et ignorabimus*," *or* be content to work on in the hope that the physical laws that underlie and explain organic Evolution may sooner or later be discovered, *or* he may seek for some hitherto hidden Law of Organism of which the known facts of Ontogenesis are the expression, and which, if accepted as a Law of Nature, would explain everything. Of the three alternatives Driesch prefers the last, which is equivalent to declaring himself an out and out vitalist. He trusts by means of his experimental investigations of the Mechanics of Evolution to arrive at "elementary conceptions" on which by "mathematical deduction"[1] a complete theory of Evolution may be founded.

If this anticipation could be realised, if we could construct with the aid of those new Principia the ontogeny of a single living being, the question whether such a result was or was not inconsistent with the uniformity of Nature, would sink into insignificance as compared with the splendour of such a discovery.

But will such a discovery ever be made? It seems to me even more improbable than that of a physical theory of organic evolution. It is satisfactory to reflect that the opinion we may be led to entertain on this theoretical question need not affect our estimate of the value of Dr. Driesch's fruitful experimental researches.

J. Burdon Sanderson.

[1] "Elementarvorstellungen . . . die zwar mathematische Deduktion aller Erscheinungen aus sich gestatten möchten." Driesch. "Beiträge zur theoretischen Morphologie." *Biol. Centralblatt*, vol. xii., p. 539, 1892.

ON RECENT ADVANCES IN VEGETABLE CYTOLOGY.

PART I.

DURING the last quarter of a century a considerable change has passed over the aspect of biology, especially in this country. It was formerly possible for a man to be, fairly at any rate, well up in the two branches of zoology and botany, but this is no longer possible, regarded from our modern standpoint. Specialisation, inevitable owing to the rapid advances which have been everywhere made, has not only effected a practical divorce between these two sciences, but the same disrupting agency is operating continuously in each of them.

None the less is it true, however, that there are certain features of fundamental importance which are shared alike by animals and plants. This community of structure is most clearly recognised within the limits of the individual cells, and it is perhaps nowhere more impressively demonstrated than in the remarkable similarity which exists between the nuclear division as observed in animals and in plants,—a similarity which may extend to the most minute details.

The cell, using the word in *its widest sense*, is, as Haeckel said long ago, emphatically the unit of life. For though the several parts, such as nucleus and the cell-protoplasm, which together constitute a cell, all possess autonomy to a certain degree, it still remains true that it is only when they operate jointly and in harmony that a successful and "going concern," a living individual, is the result. And since we have strong reasons for believing that animals and plants represent the diverging limbs of a stock traceable at the root to a common source, *viz.*, lowly unicellular organisms, it is obvious that the study of the cell, of its structure and of the functions discharged by its various parts, offers an immensely important, though it may well be a very difficult, field for research.

What, we may ask, is the essential structure of the protoplasm, of the nucleus, and of those marvellous bodies, the chromosomes, which reappear at every nuclear division? What is it that initiates the division of a cell or of its nucleus, and why do some cells go through such complex evolutions whilst others seem to adopt a relatively simple course? What is it that determines that the descendants of one cell shall develop differently from those of another, so as to give rise to this or that tissue system? Or again, how is the unicellular condition of an infusorian compatible with an intricate and often highly differentiated organisation?

These and a host of other questions rise and confront us on the very threshold of our inquiry, and the hints which Nature has dropped for our guidance are at best only obscure ones; thus the position of the biological investigator contrasts unfavourably with that of the chemist or physicist, inasmuch as he is generally debarred, owing to the very conditions of the bodies he is dealing with, from having recourse to *direct* experiment; Nature conducts the experiments and he has to remain content with watching the result, analysing the factors and reconstructing the process as best he can. Nevertheless there is, clearly, no fundamental distinction between the (so-called) observational and experimental sciences.

It is, then, only by patient accumulation and careful comparison of *all* the facts that even a proximate solution of the difficulties before us can ever be reached. Much has been done in collecting the data, and a good deal is known both as to the structure of the cell and the phases through which it passes during its existence. And fortunately one generalisation is gradually emerging with increasing clearness from beneath the ever-growing pile of detail, and it promises to prove a guide of no small value, namely, that in those processes which we have reason to regard as fundamentally important there exists a *surprising degree of similarity* between the structural elements of animals on the one hand and of plants on the other. And these points of similarity are now known to be so numerous

and so close that we are almost warranted in drawing the conclusion that the measure of the resemblance will afford a criterion as to the relative degree of importance to be attached to this or that phenomenon of cell life.

It seems almost certain that this similarity is to be interpreted as the result of the evolution along parallel lines of a particular structural arrangement, or, to put it in another way, as being the outcome of the continuous operation of similar forces upon an essentially similar protoplasmic structure. No doubt all the change manifested in protoplasm is ultimately to be ascribed to the effects of forces upon its own material substance; the special point of interest here lies in the *similarity* of the results. It cannot be due to mere accident that the stages in the development of the spermatozoa of a newt should bear a closer resemblance to the corresponding divisions in the pollen-mother-cell of a lily than they do to the rest of the tissue cells in the body of the same newt.

In the present article it is not my purpose to attempt to summarise the vast amount of detail which has accumulated within recent years; my aim is rather to try to indicate the general directions in which the results seem to be tending, and to point out the kind of evidence on which the current views are based. And although I am here especially dealing with the botanical aspect of the questions involved, it will be clear from what has been already said that it will be impossible, and certainly not desirable, to ignore the investigations which have been prosecuted by the zoologists.

And in order to make clear that which is to follow, it may not be superfluous to recapitulate the general relations of nucleus and cell protoplasm as commonly received at the present time. The essential character of all cells, whether animal or vegetable, and whether they exist as free independent organisms, or whether they form more or less highly differentiated colonies, consists in this, the association of a nucleus with a certain amount of cell protoplasm (commonly called *Cytoplasm*, to distinguish it from the nuclear protoplasm). And this is equally true, so far as we have means of determining the question, in the case of those

organisms in which we as yet have failed to recognise a definite nuclear body, for there are reasons for believing that the nuclear substance is in all cases really present, whether it happens to be collected into a specialised mass or not. And it should be remembered that the number of cells supposed to possess what we may term a distributed or discrete nucleus is becoming smaller as our means of investigations improve. Thus according to Wager (1) even Bacteria possess a true nucleus.

I am perfectly aware that attacks have recently been made on the cell-theory as extended to explain the organisation (Whitman, Sedgwick) of animals, and that nobody would assert the cell to the ultimate unit of *living substance.* But neither of these propositions really affects, or is concerned with, the point of view just now before us. We are not here dealing with the wide questions connected with the architecture of the organism as a whole, nor with the equally difficult one, as to what constitutes the ultimate units of living matter, rather we are content just now to study the interaction of the parts which together are capable of carrying on a continuous living existence, which form a living individual, and these parts consist jointly of the nucleus and its surrounding cytoplasm.[1] The occurrence of cell walls is a matter of no importance from a general standpoint, although when present they may profoundly modify the characters of the organism in which they are formed. Many plants are known in which the protoplasm is only delimited by a cell wall from the surrounding medium, while the oftentimes huge protoplasmic mass suffers no internal partitioning, although it contains a vast number of nuclei distributed through it.

Sachs, with characteristic insight, long ago perceived that the presence or absence of cell walls is a matter of only secondary importance. Their sequence and arrangement at the time of their first appearance can be predicted

[1] The researches of Klebs, Acqua, and others have shown that although protoplasm deprived of a nucleus may sometimes even assimilate food and maintain life for a not inconsiderable period of time, it is incapable of division.

from simple geometrical considerations quite independently of the ultimate form which will be finally assumed as the result of specialised growth. And in applying the word *Non-cellular* to those plants in which partition walls do not occur, he merely gives formal expression to the fact that these anatomical structures are absent, although in other respects the plants in question conform with those usually called multicellular, and they are not at all to be regarded as consisting of a single enlarged cell. In fact he has expressly stated that non-cellular plants are really the equivalent of multicellular organisms in which the formation of internal cell walls does not occur. More recently he has introduced the term *Energid* (2) to express the physiological individuality of those units I have here continued to call cells, and he thereby emphasises the fact of their real existence whether any positive anatomical boundaries can be discerned between them or not.

It must however be clearly understood that in formulating the expression energid, Sachs lays especial stress on the dynamical aspect of the relations existing between the cytoplasm and the nucleus. But it will be admitted by most people that a conception of force apart from the material substance on or through which it acts, and by which its operation becomes perceptible to the senses, belongs to the domain of purely abstract ideas. We require to know far more of the nature and structure of protoplasm before we can usefully divorce our conceptions of force from our experience of matter in attempting to ascertain the nature of those physiological causes of which all external form is but the outward and visible sign. Sachs himself, however, escapes the charge of vagueness, by restricting the application of his expression so as to impose a territorial limit to the sphere of influence mutually existing between each nucleus and the surrounding cytoplasm. For him the word Energid embodies the idea that the whole protoplasmic region is partitioned into smaller provinces each dominated by its own nucleus. And although it may be advantageous for the seprovinces to be delimited from each other by cell walls, permitting thereby a more complete independence to

attach to each one severally, the existence of such well-defined boundaries is by no means an indispensable condition of great complexity of organisation. *Caulerpa* amongst the algæ imitates very closely the differentiated form of some of the higher terrestrial plants, without however possessing their corresponding internal structure. Its protoplasm is bounded by an external wall only, and is not internally partitioned. And yet the characters distinctive of the energids in the leaf-like parts are assuredly different from those of the energids which exist in the creeping stem or rootlike fibres. A transition from the condition of *Caulerpa* to that of the higher plants may be seen in *Cladophora*, in which the filamentous body seems, at first sight, to be made up of chains of cells, each of which stands in a definite relation to the general symmetry of the branched plant; nevertheless, closer examination shows that each "cell" is multi-nucleate, and really represents a federation of energids which so act together as to constitute morphological units as far as the external form of the plant as a whole is concerned.

Sachs' conception of the energid has been assailed by some writers, and he has to some extent perhaps invited criticism by formerly affixing a quasi-morphological, as well as a physiological significance to the term. At first sight it may seem difficult to justify its application in those cases in which streaming movement happens to go on in certain layers of the protoplasm, whilst the layer in which the nuclei are embedded is at rest. It is obvious that if we admit, as we can hardly avoid doing, that the nucleus does really exert a directive action over a localised area, the migratory protoplasm (assuming the movement to affect the protoplasm, and not merely the granular bodies contained in it) must be constantly coming within the range of fresh centres of influence. It may perhaps be compared to the case of a person passing from a region presided over by one government into one under the jurisdiction of another. Such a person would naturally be subjected to changed conditions, without however affecting either his own identity or that of the particular political centres through which he may happen to travel.

Strasburger (3) has attempted to define more clearly the position of the individual energid, by proposing to limit its application to the nucleus together with a special part of the cytoplasm which he calls Kinoplasm and which he regards as the proximate seat of the effective manifestation of the forces at work in the cell. He regards the nomadic streaming protoplasm as being mainly charged with the function of providing nourishment for the nucleus and kinoplasm, and he distinguishes it by the special term of Trophoplasm. Strasburger maintains this same distinction between the active Kinoplasm and the nutritive trophoplasm in those cases in which the limits of the several energids correspond with those of the individual cells; and in this he is logical enough, for we know that living cells are not isolated from each other, but that protoplasmic continuity exists between adjacent cells by means of pores in the intervening walls. How far the distinction between kinoplasm and trophoplasm is either justified by observation or demanded by theory is another matter altogether.

But although the conception of energids is a happy one, as enabling us to distinguish discrete individualities in what may at first sight appear to consist of a common structure, it is not to be inferred that the individuals enjoy independence. The great merit of the idea lies in the fact that it serves to narrow down, and hence to render more clearly comprehensible, many important problems which call for a solution before we can hope to grapple successfully with the more advanced questions relating to those forces of a still higher order which control and apparently direct the development of the organism as a whole, or to put it in another way, which determine the course of development which the particular energids shall follow. Such control is plainly apparent at every stage in the life of an organism. Why does growth take place symmetrically so that the energids, cells, or whatever we may choose to call them, so act in unison as to produce a "body fitly joined together and compacted by that which every joint supplieth, according to the effectual working in the measure of every part"? Without some such assumption how is it

possible to account for the fact that in certain embryos which have been mutilated, the surviving cells are enabled to so modify the course of their normal development as to make good the loss, and thus to form a perfect, if somewhat miniature organism? For had there been no mutilation the cells thus concerned would unquestionably not have developed in the same way, but would have fulfilled the allotted task of merely providing for the genesis of their normal tissue products. Or again, why is it that when a lizard's tail is broken off the general *form* of the entire animal is once more reproduced, even though there are important histological and structural (but probably not functional) differences in the new tail as compared with that of the original one (4)?

When differentiation has so far become manifested in an organism that the limits of the several energids are coterminous with the cell walls, a considerable increase in their degree of independence doubtless ensues, but it is, as already stated, by no means absolute, and the examples just quoted support the statement. Whether organisation is the result of, or the factor which determines, the co-ordinate action of the cells is a question which we may safely leave to the future to decide. But perhaps it may be permissible to compare the cell colony which forms the organism to an isolated society in which the caste system prevails. Each caste or cell group is predestined to discharge certain definite offices in the state or the organism. If some indispensable caste should become exterminated, it is obvious that a differentiation and displacement must occur amongst those which survive, and this differentiation might either be readily complete, or it might only arise as a reluctant concession to necessity, just as a willow twig planted upside down in damp soil will form roots at this, its upper, end; though comparison with a twig planted with its basal end in the ground will show how severe a tax the unusual effort has proved.

It has already been said that an energid, and it might also be added, a typical cell, consists essentially of a nucleus and the protoplasm included within a certain area around

it. But we cannot as yet answer the more obvious and, one might think, almost preliminary question as to what the chief functions which are discharged by these two components really may be. It is certain that the existence of a nucleus is essential to morphological development such as is implied in the production of new cells, and very probably also in the further differentiation of those which have already been formed. Instances of this are seen for example in the growth or alteration of the cell wall. Haberlandt (5) some years ago drew special attention to the fact that when local thickening occurred in a cell wall the nucleus commonly moved to this spot, and the present writer has repeatedly observed it during the formation of the hard coat found on many seeds; here the deposition of substance is usually localised on the inner parts of the cell, and the nucleus takes up a corresponding position as soon as the process begins. Korschelt (6) has observed a similar relation to exist during the chitinisation of the membranes of insect cells, and quite recently Istvanffi (*Ber. Deut. Gesel.*, Dec., 1895) has observed that when the tubular hypha of *Mucor* branches, a nucleus is invariably present at the spot whence the branch is arising. Strasqurger (3*a*) has also drawn attention to the same truth, inasmuch as he states that before the opening of the zoosporangium of *Œdogonium*, the nucleus and kinoplasm aggregate in the vicinity of the spot at which the hole is about to be formed.

But perhaps one of the most striking instances of the directive effect of the nucleus as a whole is to be seen in the result of an experiment of Boveri, who asserts that he impregnated a non-nucleated piece of protoplasm of an echinoderm ovum with the sperm nucleus of another species;[1] development ensued, and the larva resembled the paternal form (7).

In discussing the relations which exist, or are supposed to exist, between the cytoplasm and the nucleus, it is clearly of the first importance to know what are the changes which occur in them, and especially in the nucleus, during the

[1] The animals actually employed were Echinus microtuberculatus (male), and Sphaerechinus granularis (female).

growth, maturity and senescence of the cells. Some extremely interesting results in this direction have recently been published by Zacharias (8). An ordinary resting nucleus consists, as all biologists are aware, of a somewhat dense thread-like framework, often spoken of as linin, which usually exhibits copious anastomosis, sometimes to such a degree that it almost forms a spongy texture. In this framework granules are found embedded which react definitely to stains and to solvents; they constitute the nuclein, a phosphorus-containing substance which at the periods of nuclear division undergoes an enormous increase in bulk. The linin is bathed in a more fluid substance, the paralinin. One or more spherical bodies, the nucleoli, are often present in addition to the foregoing constituents, and the nucleus is delimitated from the cytoplasm by a pellicle or membrane. The nucleolus contains, as was shown by Zacharias many years ago, at least two substances, one of which is of an albuminous nature, and is dissolved out on treatment with gastric juice; after peptic digestion has extracted the albumin, a substance is left which Zacharias calls Plastin. Now observation shows that the relative proportion of these two constituents varies considerably at different periods of the life of the cell, and this is of importance in connection with the intricate series of changes which the nucleus passes through during the process of ordinary division. The conviction has slowly been forced upon us within the last few years that there exists a considerable variety amongst the bodies which have been included in the common term of nucleoli. Auerbach (9) showed in 1890 that some of them absorbed certain red dyes with greater avidity than they did certain blue ones, whilst other nucleoli reacted in the opposite manner. He thus distinguished between erythrophil and cyanophil nucleoli. These results have been extended to plants by the investigations of Rosen (10) and others, but especially by Zacharias, who has applied the test of solvents to them, with the result that the difference between the two classes of nucleoli proves to be a much more real one than had hitherto been supposed. And these observa-

tions are specially interesting when considered from the point of view of the great dissentience of opinion which exists between most botanists and zoologists as to the nature and function of the nucleolus. Strasburger, who admitted the correctness of Rosen's statements, considered that the difference between an erythrophil and a cyanophil nucleus was largely one of nutrition, and he instanced in support of his view the difference between the erythrophil nucleolus in the nucleus of the well-nourished oosphere and the cyanophil nucleus of the much smaller, and therefore presumably worse nourished generative cell of the pollen tube. But Zacharias, in criticising Strasburger's views, considers that there is no evidence to prove that the one nucleolus is in a better position than another as regards its nutrition, and it is still more difficult to accept the suggested explanation in those cases in which both forms of nucleoli are concomitantly present.

Zacharias has shown that whereas the erythrophil nucleoli contain albumin and plastin, the cyanophil kind (the "pseudo-nucleoli" of Rosen and others) contain *nuclein*, a substance quite absent from the other class of nucleoli. Rosen in 1892 stated his conviction that his pseudo-nucleoli in reality consisted of chromatic substance (nuclein) and that they contribute to the formation of those remarkable bodies, the chromosomes, which are evolved by the breaking up of the linin framework after the amount of nuclein has greatly increased in it, previous to the division of the nucleus. Now the nucleolus exhibits striking changes both during the growth, and also during the division of the cell and its nucleus. As regards the behaviour during cell growth, the relation of the nucleolus to the other components of the nucleus is highly suggestive, and seems to support the view of those who hold that its function is largely, at any rate, nutritive.

In the embryonic tissue situated at the growing points of plants, the cells are all much alike, differentiation and specialisation only taking place behind these regions. Consequently it is possible to trace the changes which a cell exhibits during its transition from a primitive state to its adult form, and often, further, through the various stages

of senescence and death. Some cells, indeed, are not really useful to the plant of which they form a part, until they are dead, *i.e.*, till the wall of the cell alone remains, whilst from its cavity the protoplasm has disappeared.

The researches of Zacharias and of Rosen, which have recently been published, were directed especially to the behaviour of nuclei in the apical regions of plants, and their results in the main are confirmatory of each other, though the two observers were interested in rather different aspects of the same problem. The nuclei of all actively dividing cells are markedly cyanophil, and this character is especially noticeable just below the active generative cells. At first sight it may seem remarkable that in a fern root the nucleus of the large apical cell is less cyanophil than are the nuclei of the dividing segment cells which have been cut off from it. But the anomaly is only apparent, for though all the cells in the root owe their origin ultimately to the division of the apical cell, it must not be forgotten that the nuclear divisions in the segments which are cut off from it are far more frequent. The segments divide up into a very large number of cells before they finally form permanent tissue cells, and therefore it is not surprising to find that the nucleus of the apical cell, which is the ancestor of them all, contains less nuclein than the more actively dividing descendants. But there are several other significant observations which go to show that in cells which are in a state capable of further division, this faculty is correlated with the presence of nuclein in their nuclei. Rosen found in the roots of the bean and other flowering plants that after the tissues were beginning to show differentiation, the zone of cells forming the pericycle[1] retained, in their nuclei, the characters of embryonic cells, that is to say, that, whereas the nuclei of the rest were losing their cyanophil character and were becoming erythrophil, the pericyclic nuclei retained their nuclein contents. Now the lateral roots arise in this pericyclic layer, and they do so by the differentiation in it of new growing points. Hence these

[1] A zone of parenchymatous cells sheathing the more central wood and bast parts of the vascular strand.

new rootlets can only be developed from cells which still retain, or can re-awaken, embryonic characteristics. Behind the region in which lateral roots arise, the cells of the pericycle lose their cyanophil nature, and here again the loss is first apparent in those cells from which, even normally, no roots would originate, *viz.*, those situated opposite the phloem. It would be interesting to know whether in the case of those roots in which the lateral rootlets arise right and left of the protoxylem (*e.g.*, Cruciferæ) a corresponding difference obtains.

Again, Zacharias noticed that during the development of the guard-cells of the stomata in a number of leaves a similar difference held good. In a simple case, *e.g.*, many Liliaceæ, the mother-cell of the guard-cells is cut off from a cell which is destined at once to form one of the ordinary and relatively large epidermal cells. In this case, whilst the nucleus of the mother-cell of the stoma retains its nuclein contents, the other one rapidly becomes poorer in this constituent, it grows and develops a large nucleolus. The small mother-cell again divides to form the guard-cells of the stoma, and only then does a nucleolus become at all conspicuous, and the nuclein diminish in quantity. And therewith the further capacity for division ceases.

Besides the connection which is shown to exist between a nucleus which is capable of division, and its richness in nuclein, there are certain other facts of importance which demand notice. The nuclei of cells which are actively dividing are commonly characterised by the possession of smaller nucleoli than are those in which no further divisions will take place, but which are still growing in size. In fact Zacharias states generally that, as regards nuclei of cells emerging from the meristem region, the nucleoli first increase to a maximum, that this is accompanied by an enlargement of the nucleus as a whole, which however only reaches its maximum size after the nucleolus has done so, and that the latter body then diminishes faster than does the nucleus as a whole.

Further, Zacharias found that not only is the nucleolus losing substance in those cells which are specialising to

form tracheids, vessels and sieve tubes, but that the nucleus as a whole is losing, and still more rapidly, those substances which are capable of being removed by peptic digestion from the cell. The facts seem to suggest that it is albumin, or some other proteid, which is disappearing; and it is clear that the loss is due to a change in the nucleus itself, irrespective of the amount of nutrition available in the surrounding plasma, since the change is extremely obvious in the degenerating nuclei of sieve tubes, in spite of the fact that they are surrounded by abundant albuminous substances in the slimy contents of the cells. On the other hand, in those cells which are growing in size, preparatory to further divisions, such as in spore-mother-cells, the *increase* in albuminous substances, both in the nucleus generally, and especially in the nucleolus, is strongly marked. Spore-mother-cells, as a rule, pass through a relatively long period of growth, and hence we might perhaps anticipate (as we find to be the case) that they exaggerate the changes seen in the dividing and growing cells of the apical meristem. But I do not wish to lay too much stress on this, because we know that other, and profound, changes occur during the growth of spore-mother-cells, and it is uncertain to what extent the facts just mentioned may be connected with them.

It may possibly be objected that observations like those of Zacharias are open to adverse criticism on the ground that the chemistry, and *à fortiori* the microchemistry, of the proteids and other substances which occur in cells is as yet in such an unsatisfactory condition. But this objection is really not a legitimate one. We know that certain structures in the cell are differentiated by their selective action on certain dyes, and it is to this fact that their recognition was due in the first instance. But we find the action of certain solvents to yield no less definite results. Given a nucleus in a particular condition (as judged by the structure rendered visible by staining), and it will be found that the degree of solubility of its constituent substances is characteristic for the particular stage in the life history of the cell or of the nucleus which may happen to have been selected.

Hence it seems clear that the two methods ought both to be employed; for whilst the staining exhibits more or less completely the structural arrangement of the substances present, the microchemical method not only indicates some at least of the important differences which exist between the different structures revealed by the action of staining, but it teaches us that certain of these same structures are by no means so homogeneous in their nature as one might be led to suppose relying on the evidence derived from staining alone.

But those who pin their faith on stains sometimes seem to forget that they are after all only employing a sort of microchemical method themselves. For the fact that different histological elements of the cell are distinguishable by stais, implies the existence of a chemical dissimilarity between them. And this becomes the more obvious when, owing to periodically recurring changes in the cell, we assert that this or that structure is growing or diminishing. The investigator who is consciously proceeding on microchemical lines is at least not so open to the charge of mere empiricism as are those who look for salvation to hæmatoxylin or the anilin dyes. He may be wrong in supposing, for example, that the phosphorus within the nucleus only occurs in the nuclein, just as he may be in error in assuming that the substance nuclein itself really represents a chemical substance in the same way that sugar does. But he materially advances our knowledge of the cell when he determines the fact that a body which fluctuates in size as does the nucleolus, is composed of two substances or groups of substances one of which is soluble in gastric juice whilst the other is not; and that further, the relative size is, in the first instance, correlated with the amount of substance which the fermentative action of pepsin can render soluble.

It is readily conceded that the bodies we call nuclein, plastin, and the like, possibly may not, as stated already, represent chemical molecules at all. This does not, however, diminish the interest attaching to the proof that this or that substance is at one time present, while at another

time it can be no longer recognised in its former place. Nor does this observation lose in importance when the differences are shown to closely accompany changes in the general characters of the cells themselves.

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THE MORPHOLOGY OF THE MOLLUSCA.

THE recent publication of a number of new manuals and monographs dealing with the Mollusca offers a favourable opportunity for a review of our knowledge of this great phylum of the animal kingdom. It is not fifteen years since Professor Lankester's classical article on Mollusca was published in the *Encyclopædia Britannica*, yet the contributions to Molluscan morphology since that date have been not only numerous, but in many cases of prime importance.

The older method of inquiry, that of the comparison of types more or less arbitrarily selected from different groups, has been succeeded by investigations more directly influenced by the idea of evolution. The comparison of types has been replaced by the study of groups. The foundations of the morphological edifice were laid upon the former method; the superstructure and details are the result of the latter. Homologies having been to a large extent determined, we now seek phylogenies. It happens also from time to time that the detailed study of a group with the object of reconstructing the phylogeny of its members leads occasionally to the discovery that homologies based on the simple method of anatomical comparison turn out to be nothing more than analogies—recurrent examples of similar modifications.

One result of these phylogenetic inquiries has been the concentration of particular attention upon forms which are presumably the most primitive in each group; and great advances have thus been made in our knowledge. Kowalewsky and Marion, Pruvot, Wirén, and Thiele have enormously extended our acquaintance with the Aplacophorous Isopleura; primitive Prosobranchs (Docoglossa and Rhipidoglossa) have been thoroughly investigated by Haller and Boutan; Bouvier has thrown new light upon the Opisthobranchia by his researches on *Actæon;* Boas and Pelseneer have revolutionised our ideas of the Pteropoda

by their work upon *Limacina* among the Thecosomata, and upon *Dexiobranchæa* and other types among the Gymnosomata; the morphology of the Pelecypoda has been further elucidated by Pelseneer's observations upon *Nucula* and other primitive forms, and important contributions to our knowledge of the Cephalopoda were made during the past year by Huxley and Pelseneer in the case of *Spirula*, that last survivor of the ancient types of Decapod Dibranchiates. We doubt if any equivalent group of the animal kingdom, except perhaps the Echinoderma, has been the subject of such productive researches as the Mollusca during the period under consideration; and certainly the phylogenetic method of inquiry has attained no greater triumphs than in the hands of Bouvier, Haller, Pelseneer, and other investigators of the Gastropod and Lamellibranch series.

In the present article I propose to deal more especially with recent contributions to our knowledge of the Molluscan nervous system, reserving a fuller consideration of other questions for a later article.

There is one writer, however, whose views must first of all be dealt with, as on a great number of fundamental points they are opposed to all current conceptions of Molluscan morphology. These views merit some detailed consideration, moreover, for they are based on propositions which are not without a certain appearance of plausibility, and may well serve as test-questions by which to examine into the accuracy of the homologies which have been generally admitted to exist between the different sections of the Molluscan phylum.

Thiele has published his views in a series of lengthy papers, the references to which will be found in the bibliography (23, 24, 25). He regards the Mollusca and Annelida as direct descendants of Polyclad Turbellarians, and his identifications of homologous organs in the different Molluscan groups are determined, not by a direct comparison of the organisation of these types one with another, but by independent comparisons of the organisation of the different Molluscan types with that of sucker-bearing Polyclads. The group Mollusca is thus made to lose its

compactness, and characteristic organs, such as mantle and ctenidium, which have been regarded as homologous throughout the Molluscan series, are interpreted in different ways in the different types, as the exigencies of Thiele's theory demand. One of the first propositions assumed by this writer is that the foot of the Mollusca is simply a colossal enlargement of the ventral sucker of the Polyclad; the suctorial function of the foot in *Chiton* and the lower Gastropoda is pointed to in support of this comparison. A series of more revolutionary propositions is then promulgated in consequence of the necessity under which the author is placed of discovering the primitive body-edge of the Mollusca comparable to the edge of the body of the Turbellaria. This primitive body-edge Thiele identifies by means of the lateral sense-organs which characterise the epipodium in the Rhipidoglossa and the margin of the mantle in Pelecypoda. The epipodium in Gastropoda and the mantle edge in Pelecypoda are thus taken by this writer to represent the sides or edge of the body in the Turbellarian ancestor. The epipodium in Gastropoda and the mantle edge in Pelecypoda consequently separate the dorsal from the ventral regions of the body in those groups. It follows from this that the ctenidia of Gastropoda, which are supra-epipodial in position, are not homologous with the ctenidia of Pelecypoda, which are infra-pallial. How we are to regard the anus, which is dorsal in the one group and ventral in the other, is not explained. But since in operculate Rhipidoglossa the operculum, like the shell, is situated above the epipodium, we are told that the operculum must also be regarded as dorsal in position, as well as serially homologous with the shell proper. This, in Thiele's eyes, compares well with the condition of affairs in *Chiton*, whose shelly plates are without doubt serially homologous. Moreover, although the existence of an epipodium in *Chiton* has not been hitherto recognised, Thiele argues that, since the pallial fold in this form represents the primitive body-edge, it must also, together with the series of ctenidia which are attached to its lower surface, be regarded as the homologue of the epipodium of the

Rhipidoglossa. The ctenidia of *Chiton* are, in fact, regarded as modified epipodial cirri. The consequence of this view is that while the mantle of *Chiton* and the mantle of Pelecypoda are regarded as homologous, the mantle of the Gastropoda is supposed to represent only a portion of the mantle in these other forms, and its projecting rim, similar as it appears to be in the two cases, is held to be a new and secondary formation unrepresented in the Amphineura and Pelecypoda.

Nowhere, however, do we find in Thiele's voluminous writings any explanation of the anomaly which ought to have occurred to him, that while in *Chiton* the anus is "ventral," and lies well beneath the "epipodium" and the last shell-plate, in operculate Gastropods the intestine opens not only above the epipodium, but between the operculum and the shell of the embryo—a relation which could only be represented in *Chiton*, if Thiele's theories were correct, by the situation of the anus between two of the shell-plates upon the back of that animal!

The nervous system of the Mollusca is treated by Thiele with a ruthlessness no less than that which is meted out to the external organs of the body. Let us take the Amphineura first. In this group, if the relations of the nervous system in *Chiton* be taken as typical, we have dorsal to the gut a great ganglionic nerve-ring whose lateral components are usually referred to as the lateral or pleuro-visceral cords. Connected anteriorly with the cerebral enlargements of this nerve-ring is a pair of ventral or pedal cords, connected with one another by a series of commissures lying beneath the gut, and also with the lateral cords by means of lateral connectives. The lateral cords innervate the pallial sense-organs, gills, and viscera; the ventral cords the musculature of the foot. The lateral cords are regarded by Thiele as the homologues of the lateral cords or nerve-ring of the Turbellarians, and the ventral cords are taken to correspond to the ventral longitudinal nerves of the same forms. So far we find nothing either erratic or original, for the same view has already been taken by Lang (16).

But the novelties begin with Thiele's interpretations of the nervous system of Gastropoda and Pelecypoda. We have already pointed out Thiele's view that the epipodium of Gastropods represents the primitive body-edge. Now at the base of the epipodium in *Fissurella* and *Haliotis* there lies a ganglionic plexus; and this plexus, which takes the form of an incomplete ring, is regarded as the homologue of the lateral cords of Turbellarians and Amphineura. The series of epipodial nerves which connect the epipodial plexus with the upper half of the pedal cords in Rhipidoglossa is compared with the series of connectives between the lateral and ventral cords in Amphineura.

This seems very plausible until one recollects (1) that, the epipodium being infra-rectal, the epipodial plexus is also infra-rectal and thus difficult to compare with the lateral cords of Amphineura, whose "commissure" is supra-rectal; and (2) that, whereas in Amphineura the lateral cords innervate practically the whole of the pallium and viscera, in Rhipidoglossa the epipodial plexus has nothing to do with any other organs except the sense-organs of the epipodium. If the pallium of the Gastropoda is really, as Thiele maintains, a secondary differentiation of the primary pallium of the Amphineura, one would expect that its innervation would also be effected by progressive differentiation of the nerve-centres which supplied the primary pallium, *viz.*, from the lateral or epipodial centres. So far from this being the case, however, Thiele himself (xxv., pp. 587-9) adopts the view that the pallial nerves as well as the pleural ganglia of Gastropoda are secondary derivatives of the ventral or pedal cords.

The recklessness of Thiele's comparisons reaches its high-water mark, perhaps, in his remarks on the nervous system of Pelecypoda. Correlated with the existence of numerous sense-organs (eyes, tentacles, etc.) along the mantle edge, there exists in many forms (*Arca*, *Pecten*, *Pinna*, etc.) a nervous ring around the mantle which may take the form either of a complete ring of peripheral ganglia united by a plexus, or of a circumpallial ganglionated nerve, as was recognised by Duvernoy (5) more than thirty years

ago. Since the mantle-lappets of the two sides of the body unite posteriorly above the anus, this pallial nerve-ring lies above the gut. The ring is connected with the cerebro-pleural ganglia by means of the anterior pallial nerves, and with the visceral (parieto-splanchnic) by means of branches from the great posterior pallial nerves. Accordingly Thiele homologises the circumpallial nerve-ring with the lateral cords of *Chiton* and with the epipodial plexus of the Rhipidoglossa.

The first of these homologies seems not unreasonable, for no one disputes the homology between the mantle of *Chiton* and that of Pelecypoda. Moreover Kowalevsky's discovery that *Chiton* in its later embryonic phases is provided with a pair of transitory eyes which lie outside the velar area and have some close connection with the lateral nerve-cords, renders this comparison particularly worthy of attention. But how the circumpallial nerve of Pelecypoda can be in any sense homologous with the epipodial plexus of Gastropoda, when the latter structure lies beneath the gut and has no connection with the cerebral ganglia, either directly or by the intermediation of the pleural ganglia, it is altogether impossible to conceive. And this is not all. The posterior connection between the circumpallial nerve of Pelecypoda and the visceral ganglia is compared by Thiele with the posterior connectives between the lateral and ventral cords of Amphineura; and the time-honoured visceral nerve-cords of Pelecypoda, with the visceral (parieto-splanchnic) ganglia upon them, are homologised with the ventral cords of the Amphineura. To reveal the absurdity of these comparisons it is sufficient, I think, to remind my readers that the ventral cords of *Chiton* are concerned exclusively with the innervation of the musculature of the foot; while the visceral cords of Pelecypoda innervate the body-wall, ctenidia and viscera, in addition to the posterior adductor muscle. How these supposed homologues of the ventral cords of *Chiton* have come to assume so many of the functions of the lateral or pallio-visceral cords, is not explained; and since Pelecypoda possess a pair of pedal ganglia in the foot, as typical in their relations

as those of any Gastropod—in *Nucula* to the extent even of having separate cerebro-pedal and pleuro-pedal connectives (18, 19)—it seems profitless to pursue these ill-balanced speculations any further.

The utmost ingenuity cannot overcome the fact that there is a fundamental disparity between the Turbellarian and Molluscan body. This disparity is revealed by embryology; but to embryology Thiele pays scant attention. Thiele's argument is practically this (24, p. 504),—that the only route from Cœlenterates to Bilateralia is *viâ* the Ctenophores to Polyclads, and that Annelids and Molluscs are consequently to be derived from Polyclad ancestors. Embryology seems to me, however, to point to two lines of descent at least, from the Cœlenterates to the Bilateralia. In each case the oral surface of the Cœlenterate ancestor became the ventral surface of the Bilateral descendant; but along one line of descent the primitive mouth or blastopore retained its ancestral form as a simple circular orifice in the middle of the ventral surface, and opened into a gastral cavity devoid of an anal orifice (Polyclads); while along the line of descent which led to the Annelida and Mollusca the blastopore elongated along the ventral surface, as Sedgwick has so ably contended, its lips coalesced except at the two extremities, and these open ends constituted the mouth and anus of the Cœlomate descendants. Thiele has altogether overlooked the significant behaviour of the blastopore in Annelidan and Molluscan embryos; and since no similar modification of the blastopore is known in the case of Turbellarians and Trematodes, in which groups the absence of an anus is so marked a characteristic, we are amply warranted, I think, in drawing the conclusions which I have emphasised above.

The admission of this distinction is however fatal to any theory of the Polyclad ancestry of the Mollusca. The foot of the Mollusca is a development of the fused lips of the elongated blastopore, and can in no case be homologised with the ventral sucker of Turbellarians which lies entirely behind the blastopore. The same remark applies to Lang's comparison of the Molluscan foot with the ventral

surface of the Turbellarian. The foot is undoubtedly part of the ventral surface of the Mollusc, and as such may be compared, in a general way, with the creeping surface of a Planarian ; but as a specialised organ, developed from the fused lateral margins of a slit-like blastopore, it has no homologue in the organisation of the Turbellaria.

Let us now see what light has been thrown on the problems of Molluscan morphology by the researches of other investigators.

The visceral commissure.—One of the greatest difficulties in comparing the Amphineura with the Gastropoda or other Molluscan types has long been the fact that the lateral or pleuro-visceral cords of *Chiton*, which innervate the gills, viscera, and mantle, are united to one another posteriorly by a "commissure" lying above the rectum ; whereas the visceral commissure of Gastropoda and Pelecypoda, etc., lies below the intestine.

A little care in the use of words would have prevented much of the confusion and controversy which has arisen on this subject of the position of the visceral commissure. Words, as Bacon phrases it, put constraint upon the intellect, and there is no doubt that the disagreement and perplexity of naturalists concerning this point have been caused by one of the *idola fori* which they have themselves set up, rather than by any intrinsic incompatibility in the facts themselves. If the language must still be maintained, I must at least point out that there are commissures and commissures, and that one may be a commissure in fact, and another only in name. The suprarectal "commissure" in Amphineura is ganglionic, and, like the rest of the pleuro-visceral nerve-ring, is formed *in situ* by delamination from the ectoderm (15). It is not a commissure in the strict sense of the word, but an integral portion of an annular central nervous system. But the visceral loop of other Molluscs consists merely of nerve-fibres connecting usually a couple of visceral ganglia with one another, and with the pleural ganglia. Now nerve-fibres are outgrowths from nerve-cells, and if two groups of nerve-cells should happen to take a somewhat deep-seated position in the body

before their fibres have grown out (which is not a rare embryological phenomenon), there should be nothing incomprehensible in their fibres taking the shortest route and meeting beneath the gut instead of over it. Clearly, therefore, the ventral position of the visceral commissure in most Mollusca by no means precludes the possibility of the essential homology between the visceral loop of these forms and part of the pleuro-visceral ring of Amphineura.

The other differences between the visceral loop of most Mollusca and the pleuro-visceral ring of Amphineura are principally differences in the degree of segregation and concentration of ganglion-cells and nerve-fibres. The pleuro-visceral ring of *Chiton* represents a very primitive nervous system, characterised by the more or less even diffusion of ganglion-cells over the whole length of the cord, while the nerves arising from it are not united into large trunks, but are given off at repeated intervals in a manner which is almost metameric. The nerves springing from it innervate the same parts of the body as the combined pleural and visceral ganglia of Gastropods and other Molluscs, *viz.*, mantle, ctenidia, intestine, heart, nephridia, and gonads. But if, after the reduction of the ctenidia to a single pair, we imagine a process of segregation to set in between these various elements, the more strictly visceral centres would become separated from the superficial pallial centres, and would assume a deeper position in the body. The law of concentration would apply in this as in other cases of evolution of nervous systems (3), and the result of the whole process would be the differentiation of a visceral nervous system, consisting of ganglia and commissural fibres, out of the primitively mixed and diffuse pleuro-visceral system. If the primitive relations to the gut and ring-like form were retained at all, they would be retained, not necessarily by the visceral system, which has *ex hypothesi* undergone considerable changes, but by the pallial (= pleural) system, which has undergone no change, except possibly one of incipient concentration.

The position of the commissural fibres of the visceral ganglion in relation to the gut becomes a matter of sub-

ordinate importance if the evolution of the nervous system has proceeded upon these lines, as will be made evident later on. As a matter of fact the visceral commissure is situated below the gut—a relation which is possibly foreshadowed in *Chiton* by a connection beneath the gut of the two gastric nerves described by Haller (8).

Pelseneer (19) indeed goes so far as to identify these gastric nerves of *Chiton* with the visceral commissure of Gastropoda and Pelecypoda; but the considerations which I have emphasised above show that the typical visceral nerves and commissure have not yet arisen in the Amphineura; they do not arise, in fact, until the branchial, nephridial, genital and enteric branches of the primitive pallio-visceral cords are all united into one common trunk. There is some doubt, moreover, as to the existence of the gastric nerves described by Haller, since two investigators, Plate (20) and Thiele, have been unable to discover them in species of *Chiton* examined by themselves.

A valuable contribution to this part of the subject is contained in Haller's recent *Studien* (11). In the common cyclobranchiate types of Limpet the pallial nerves are separate from one another behind, and seem to be mere outgrowths of the pleural ganglia (Bouvier, 3, p. 19); but in *Lottia*, one of the more primitive monobranchiate forms, Haller shows that the pallial nerves of the two sides are directly continuous with one another posteriorly, and make a complete arch round the edge of the mantle. They are moreover not mere nerves, since they consist of a core of fibres surrounded by an outer coating—discontinuous, it is true—of ganglion-cells. They are clearly the posterior continuations of the pleural ganglia, and represent the remainder of the pallio-visceral nerve-ring of the Amphineura after the separation of the visceral elements. This view is further borne out by the existence of several connectives between the pallial ring and the pedal cords in addition to the stout ganglionic connective which in higher forms becomes the persistent pleuro-pedal connective.

The pleural ganglion.—Haller's discovery recorded in the preceding paragraph shows clearly the error of the

view by which the pleural ganglion is regarded as a derivative of the pedal cords (Bouvier, Pelseneer, etc., *passim*). This view is founded on the fact that in the lower Gastropoda (Docoglossa and Rhipidoglossa) the pleural ganglia are directly continuous with the anterior ends of the pedal cords, while in the higher types the pleural ganglia gradually move further and further away from the pedal ganglia, and, travelling along the cerebro-pleural connectives, eventually come into contiguity with the cerebral ganglia (Tenioglossa) or even fuse with them to form a single cerebro-pleural ganglion on each side (Pelecypoda).

The close connection between the pleural and pedal ganglia in the lower forms may now be interpreted in a different manner. The ganglion-cells which were primitively distributed over the whole extent of the pallial nerve-ring have been concentrated at the anterior extremities of its lateral portions, as Haller's observations on *Lottia* show—or rather in the region of the first pleuro-pedal connective, for the most anterior portion of the primitive pallial cords is represented by the cerebro-pleural connective. The shortness of the pleuro-pedal connecting piece and the great concentration of ganglion-cells which takes place at its two extremities prevent any sharp demarcation between the pleural and pedal ganglia in these lower forms; but a comparison of the nervous system of *Lottia* with that of *Chiton* (Thiele, 23, p. 387) leaves no room for doubt as to the correctness of this interpretation, which throws a flood of light upon numerous other points which have been difficult to understand upon the older views. It explains, for example, why the cerebro-pleural and cerebro-pedal connectives should be already distinct from each other in the lower Gastropods at a stage when the pleural ganglia are in actual continuity with the pedal cords, and it sets at rest the controversy as to the meaning of the lateral furrow in the pedal cords of Rhipidoglossa which has been waged with so much skill in the rival pages of the *Archives de Zoologie* and the *Bulletin Scientifique de la France et de la Belgique*.

Development of the pleural ganglion.—That the pleural ganglion is essentially distinct from the pedal is, I think, sufficiently clear from the facts of development. Although these ganglia are placed so close together and are so intimately connected in the lower Gastropods there is not a single case on record in which the pleural ganglion has been observed to arise from the pedal ganglion, or from a common pleuro-pedal rudiment in the embryo. It is equally true on the other hand that Sarasin's derivation of the cerebral and pleural ganglia from a common rudiment in *Bithynia* (the cephalic sense-plate) has been opposed by v. Erlanger, who shows that all the great ganglionic centres arise separately, and do not become connected with one another until after their differentiation (7).

A renewed investigation of the origin of the cerebro-pleural ganglion in Pelecypoda would be of great interest in this connection. Pelseneer's (18) observations on *Nucula* have placed the fact of the composite nature of this ganglion in Pelecypoda beyond all doubt; and still, to the best of my knowledge, no one has yet observed the appearance in the embryo of a pleural element distinct from the main body of the ganglion. This apparent community of origin of the cerebral and pleural ganglia in Pelecypoda may be compared with the direct continuity of the cerebral and pleural elements of the nervous system in Amphineura.

Development of the visceral ganglia. — Sarasin endeavoured to show that the visceral ganglia of *Bithynia*, together with the pedal and abdominal ganglia, arise in the embryo from a common ventral proliferation of the ectoderm which he compares with the ventral ganglionic chain of Annelida. On this point also Sarasin has been corrected by v. Erlanger, who shows that all these ganglia arise separately from one another in *Bithynia* (7), as well as in *Paludina* (6).

The visceral ganglia are also quite distinct from the pleural ganglia in their origin, as v. Erlanger's observations show. In one important respect, however, the visceral ganglia and the pleural ganglia betray a marked similarity, the significance of which seems, however, to have escaped

the attention of its discoverer. In *Paludina* v. Erlanger figures the pleural ganglia arising from the ectoderm on each side of the body at a point just outside the velar area, but in actual contiguity with the cells of the ciliated ring. In *Bithynia* (7, Taf. xxvi., fig. 16) he figures the same condition of things for the pair of visceral ganglia. The only difference in origin between the two ganglia is that the visceral ganglia arise behind the pleural ganglia. If the Molluscan veliger possessed a nerve-ring beneath its prototroch (velum), as occurs in the trochosphere of the Annelida, it is quite clear that the pleural and visceral ganglia of *Bithynia* and *Paludina* would represent a series of ganglionic thickenings along the course of the nerve-ring. Apart from this inference, however, the topographical relations to which I have called attention seem sufficient to establish the proposition that the pleural and visceral ganglia, and, as I shall show directly, the abdominal ganglion also, of Gastropods—and, therefore, of other Mollusca—belong to a group of dorso-lateral nerve-centres quite distinct from that which is represented by the ventral or pedal cords. Here again we are reminded of the direct continuity of the pleural and visceral nerve-centres in the Amphineura.

Development of the abdominal ganglion.—In *Chiton*, as Kowalevsky has shown (15), the unpaired abdominal ganglion, or, as it is often called, the visceral ganglion, arises by a proliferation of the ectoderm at the hinder pole of the embryo, dorsally to the site of the future proctodæum. In the adult this ganglion is simply a special concentration of ganglion-cells on the supra-anal portion of the pleuro-visceral ring.

The abdominal ganglion of Gastropods is also situated at the hinder end of the visceral loop, but lies of course ventral to the gut. Can these two ganglia be regarded as homologous?

If Molluscs were mere mechanical models the answer would be undoubtedly in the negative; but embryology points unhesitatingly to the opposite conclusion. Von Erlanger has shown that in *Bithynia* as well as in *Paludina* the abdominal ganglion develops as an ectodermal pro-

liferation of the floor of the mantle-cavity, *i.e.*, that the ganglion is essentially a dorsal ganglion. Its final situation on the course of the sub-intestinal nerve-loop is rendered possible by the fact that its connectives with the visceral ganglia are not delaminated from the ectoderm, as are the ganglionic pleuro-visceral cords of *Chiton*, but are mere fibrous outgrowths from the ganglia themselves. Embryology is thus in complete accord with the views which have been maintained in the earlier part of this paper as to the homologies and origin of the visceral nervous system in Mollusca.

The pallial and visceral commissures in Cephalopoda. —It has long been known (Hancock) that in many Cephalopoda the stellate ganglia on the pallial nerve-cords are connected with one another above the gut by a transverse commissure. Is this commissure a relic of the pallio-visceral nerve-ring of the Amphineura and homologous with the pallial ring of *Lottia*, or is it merely a secondary connection?

In *Spirula* a remarkable arrangement of the pallial commissure has been recognised by Huxley and Pelseneer in their recent memoir (12). The commissure is not in this case a straight transverse band, but consists of two curved cords which arise from the right and left stellate ganglia respectively, and at their junction in the median line of the body give off a median pallial nerve which runs for a short distance forwards, and then passing over the anterior margin of the shell—which is, of course, internal—becomes recurrent and runs along the part of the mantle contained within the last chamber of the shell. Pelseneer is thus led to regard the commissure with its median nerve as formed by the two original pallial nerves fused together. The connection between the stellate ganglia having thus arisen in the primitive Dibranchiates (apparently in connection with the reduction in size and enclosure of the chambered shell), higher forms show a series of stages in its subsequent degradation, until it is finally lost in the Octopoda. The absence of a pallial commissure in *Nautilus* also supports Pelseneer's view that in Cephalopoda this structure is not of any primary importance.

At the same time when Pelseneer added a paragraph to the effect that the supra-rectal commissure of the Amphineura is also a merely secondary junction of the pallial nerves, he was probably not yet acquainted with Haller's work on *Lottia*, and allowed his views upon the Polychæte ancestry of the Mollusca to bias his interpretation of the Molluscan nervous system.

In a recent paper on the anatomy of *Nautilus* Mr. Graham Kerr (13) also refers to the question of the supra-rectal commissure. It will be remembered that in *Nautilus* the pleuro-visceral ganglia of the two sides form a stout ganglionic band encircling the œsophagus in the region of the cerebral ganglia. The pallial nerves radiate from the lateral portions of this half-ring, and the pair of visceral nerves arise from the ventral portion. The visceral cords pass backwards on either side of the vena cava, and, after giving off the branchial nerves, are prolonged posteriorly as far as the post-anal papilla, behind which Mr. Kerr has recognised an apparent anastomosis. Mr. Kerr adds that in this case "the homologue of the pleuro-visceral cord of *Chiton* is not merely the posterior sub-œsophageal nerve-mass, but rather the two lateral portions of this, together with the post-branchial prolongations which run on either side of the vena cava. The mesial part of the posterior sub-œsophageal nerve-mass would therefore be a secondary fusion between the nerve-masses of the two opposite sides."

In his suggested homology of this possible post-anal (*i.e.*, supra-rectal) commissure of the visceral nerves in *Nautilus* with the supra-rectal "commissure" of *Chiton*, Mr. Kerr has undoubtedly failed to appreciate the true nature of the posterior sub-œsophageal loop of *Nautilus*, as well as the relation of the visceral nerves to the pleuro-visceral cords of *Chiton*. The explanation of the Cephalopod nervous system is most readily found by comparing it with that of *Dentalium*, whose organisation in many respects supplies connecting links between that of the Cephalopoda and that of the primitive præ-torsional Gastropod or primitive Pelecypod. In *Dentalium* (22, p. 401) we find

a pair of post-anal prolongations of the visceral nerves precisely resembling those described by Kerr in *Nautilus;* yet in *Dentalium*, owing to the smaller degree of concentration or cephalisation which has taken place in the nervous system, it is easy to see that the typical sub-intestinal visceral commissure exists as in Gastropods and Pelecypods. The posterior sub-œsophageal nerve-mass of Cephalopods has clearly been produced, not, as Mr. Kerr suggests, by a secondary fusion of the pleuro-visceral nerve-masses of the two opposite sides, but by a simple shortening of the visceral loop as it occurs in *Dentalium.* This would bring the visceral ganglia into continuity with the pleural ganglia and with one another,—a process of condensation with which we are already familiar in the Tenioglossa and the Euthyneura among Gastropoda.

It may here be mentioned that Willey's simultaneous account (26) of the visceral nerves of *Nautilus*, while confirming Mr. Kerr's observations as to the existence of post-anal prolongations of a pair of visceral nerves, differs from his statement as to their origin. Willey states that the nerves supplying the post-anal papilla arise independently from the sub-œsophageal visceral loop, although at their origin they are adjacent to the branchial nerves and for a large part of their course are actually contiguous with them. The significance of this separation is not remarked upon by Willey; but if the separation really exists it is certainly a difficulty in the way of his contention that the post-anal papilla represents an approximated posterior pair of branchial sense-organs, since the anterior osphradium and both gill-plumes are all innervated from the outer visceral nerve.

Euthyneurism.—Since the publication of Spengel's paper on the olfactory organ and nervous system of Mollusca, a division of the Gastropoda into two groups, the Streptoneura and the Euthyneura, has been generally adopted. This classification has been accepted, moreover, not merely as an expression of the anatomical facts concerning the condition of the visceral loop in the two groups, but as a classification of phylogenetic significance. It is to be in-

ferred that the two groups have been independently derived from a common type of archi-Gastropod, possessing an untwisted visceral loop—the Prosobranchs (Streptoneura) by the twisting of the loop, the Opisthobranchs and Pulmonates (Euthyneura) by the mere shortening and concentration of the untwisted loop. This view derives support from the fact that the persistent ctenidium retains its primitive position on the right side of the body in Opisthobranchs, while in Prosobranchs it shows a marked displacement and lies on the left side. Bouvier's observations on *Actæon* (= *Tornatella*), however, have completely altered the position of affairs. *Actæon* is a very primitive Opisthobranch, as may be inferred from the high development of its shell, the persistence of its operculum, and the absence of pleuropodial fins. Bouvier tell us (4) that *Actæon* resembles the Prosobranchs, not only in these points, but also in possessing a distinct twist of the visceral loop (streptoneurism, chiastoneurie). The ctenidium is innervated from a supra-intestinal ganglion, which lies on the left side of the body. We are accordingly led to the conclusion that the euthyneurous condition of Opisthobranchs and Pulmonates has not been directly inherited from the orthoneurous ancestors of the Gastropoda, but has been derived from a previously streptoneurous condition. In other words the Opisthobranchs and Pulmonates have descended from Prosobranch ancestors, and the right-sided position of the gill-plume in Opisthobranchs is not primitive, but the result of a secondary process of detorsion.

Orthoneuroidism.—Without going further into the matter it may also here be mentioned that the supra-intestinal commissure has been recently discovered in various species of *Nerita*, *Neritina*, and *Navicella* by Boutan (2), Bouvier (3*a*), and Haller (11)—a discovery which destroys the last refuge of orthoneurism in Prosobranchiate Gastropods. Streptoneurism may now be affirmed of all Prosobranchiate Gastropods.

Origin of the Molluscan nervous system.—The attempts of previous writers to explain the relations of the nervous system of Mollusca have been based almost exclusively

upon comparisons with the fully constituted nervous systems of such types as the Turbellaria and Annelida. With Thiele's theory of the Turbellarian ancestry of the Mollusca I have already dealt, and I do not propose to deal with the Annelidan hypothesis, since this theory cannot provide any satisfactory explanation of the high development of the pleuro-visceral nervous system of the Mollusca. Those authors who, like Thiele and Pelseneer, homologise both the pleural and pedal centres of the Mollusca with the ventral cords of Annelids, base their view upon the supposed origin of the pleural centres from the pedal cords. This derivation I have already shown in this article to be completely erroneous. Pelseneer's theory of the origin of the Mollusca from Polychæte ancestors (18*a*), and all theories which seek the origin of the Mollusca in the specialised representatives of any of the vermiform groups, may at once in my opinion be dismissed from consideration.

Apart from matters of minor importance it will, I think, be conceded that the following cardinal points in regard to the morphology of the Molluscan nervous system have been established by the facts and arguments which have been presented in this article:—

(1) That the pleural ganglia have not been derived by segregation from the ventral or pedal cords.

(2) That the pleural, visceral, and abdominal ganglia of Gastropoda form a group of dorsal nerve-centres—the two former owing to their differentiation in the immediate neighbourhood of the velum, and the latter owing to its differentiation from the mid-dorsal wall of the body (floor of mantle-cavity).

(3) That the dorso-lateral nerve-ring of Amphineura is primitive and is represented in other groups of Mollusca by both the pallial and visceral nerve loops, or their derivatives.

(4) That the sub-intestinal position of the visceral loop in all groups except the Amphineura is a secondary one, which has been rendered possible

only by the decentralisation of the primitive pleuro-visceral nervous system, and its separation into special ganglia and nerves, the latter being formed ontogenetically as fibrous outgrowths from the ganglionic centres.

Venturing now, in conclusion, upon more speculative ground, I believe that the embryonic relations, to which I have drawn attention, between the pleural and visceral ganglia and the ciliated band are of phylogenetic importance. It has long puzzled me that the larval forms (trochospheres) of two groups so closely allied as the Annelida and Mollusca, while presenting a close similarity in general structure, should differ so remarkably in regard to their nervous system. The Annelid trochosphere has a nerve-ring beneath its ciliated band, while the Molluscan trochosphere has none. In this respect the Molluscan trochosphere appears to be less primitive than that of the Annelida. The explanation of this now appears to me to be as follows. In the evolution of the Annelida the prototroch and nerve-ring remained for a long time unmodified, and did not share in the elongation of the postero-ventral region of the body which gave rise to the trunk of the Annelid. This would explain the absence of the dorsal nerve-ring in the adult Annelid, provided that the nerve-ring, together with the prototroch, came to have merely a larval significance,—as actually happens in the ontogeny of Annelids to-day. On the other hand, in the evolution of the Mollusca from the same simple type of ancestor, the whole body must have shared in the elongation—the prototroch and nerve-ring as well as the more ventrally placed parts of the body. This elongated nerve-ring I identify with the pleuro-visceral ring of Amphineura, although the phyletic connection between the nerve-ring and the ciliated band is inferred from the development of certain Gastropods rather than from the Amphineura themselves. As a larval adaptation for conveniences of natation I imagine that a separation became gradually effected in embryonic life between the ciliated ring and the nerve-ring, the former becoming restricted to the anterior end of the larval body,

while the latter became more and more extended *pari passu* with the elongation of the trunk. Such a separation is to some extent paralleled in the development of Holothurians from the *Auricularia* larva, as described by Semon. On this theory alone can I explain to myself the absence of the ancestral nerve-ring in the trochospheres of Mollusca, and I find some support for this view in the ontogeny of Nemertines. The lateral nerve-cords in this group have the same relation to the gut and brain as have the pleuro-visceral cords of *Chiton*, since they form a dorso-lateral ring, the posterior commissural portion passing above the rectum. In Nemertines there can be very little doubt that this nerve-ring has been derived phyletically by the elongation of a nerve-ring which underlay the ciliated band of a more or less *Pilidium*-like ancestor, as it underlies the ciliated band of the *Pilidium*-larva, although this phyletic origin is disguised by the profound metamorphosis which breaks the continuity of the ontogenetic record in Nemertines. On this theory of course the lateral cords of Nemertines do not correspond to the ventral cords of Annelids. The latter are represented by the general ventral plexus of Nemertines and by the pedal plexus or cords of Mollusca. These ventral nervous systems appear to bear relations to the dorso-lateral ring-nerve similar to those of the subumbrellar plexus of Medusæ to the circumferential nerve-ring.

It will be recognised from these remarks that the conclusions to which I have arrived present distinct points of agreement with those of Balfour (1, p. 378) and Sedgwick (21) on the same subject, although attained throughout by an independent series of inductions. With both these writers I agree in tracing back the Molluscan nervous system to a primitively annular type, such as might be expected to exist in a Cœlenterate ancestor. Balfour derives the whole Molluscan nervous system from a peripheral nerve-ring which followed the course of a hypothetical ciliated ring; Sedgwick derives it from a broad plexus surrounding an elongated blastopore, such as occurs in existing Actinians. Sedgwick's theory was practically an alternative to Balfour's, but I find myself able to give a

partial acceptance to both these views. For the nervous system of Mollusca appears to me to consist of two parts, a circumferential ring and a peri-blastoporal plexus. The circumferential ring, which was primitively associated with a ciliated ring, is represented by the pleuro-visceral nervous system, which I have shown to possess significant relations with the velum or prototroch of the larva; and the peri-blastoporal plexus seems to me to be recognisable in the pedal nervous system, which in primitive Molluscs has a very diffuse plexus-like arrangement, and in Amphineura, at any rate, reveals its peri-blastoporal character in the cerebro-pedal connectives in front and its connectives with the supra-rectal abdominal ganglion behind.

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THE RESERVE MATERIALS OF PLANTS.

(Concluded.)

THE position of the glucosides in vegetable metabolism has been for a long time a subject of considerable controversy, which has, however, been most largely concerned with tannin. The details of its formation, its localisation and its fate have been discussed at great length, but the discussion has been largely conducted on the lines of hypothesis and analogy rather than experiment. The conclusions reached by such a method of treatment have somewhat hastily been applied to all glucosides, as if tannin were eminently the typical one. There are now reasons for thinking that so far from this being the case it is especially exceptional.

The number of glucosides known has increased considerably in recent years as our investigations into plant metabolism have been pursued, and increasing knowledge of them forces the conviction more and more upon us that they take a more or less active share in the nutritive processes, possibly direct, but more probably through certain of the products to which they give rise on decomposition. They are not so markedly reserve stores for seeds as are many of the bodies we have already discussed, though many seeds, and notably many of those of plants of the Rosaceæ and Cruciferæ and orders allied to these, contain them in quantity together with other reserves. They occur, however, in other parts of the plant, not quite as circulating reserves, but rather as transitory stores for more localised growth and nourishment. The old advocates of their nutritive functions rested their case largely on the presence of sugar in the glucoside molecule, and held that this is the body which is available for the constructive processes of the organism. There are, however, reasons for holding that this view is too limited a one, and that some of the other products of their decomposition may be as valuable as the sugar, if not of even greater importance.

The glucosides that have attracted most attention during recent years are those which occur in the plants belonging to the families already mentioned, the Rosaceæ, the Cruciferæ, and other orders which show affinities with these. These plants contain, very widely distributed through their tissues, *amygdalin* and *sinigrine* or myronate of potash respectively. Of these the former is perhaps the most interesting, as from its decomposition by enzyme agency there is produced hydrocyanic acid, which has always been regarded as most virulent in its action upon all living things. The existence of this noxious principle in the plant has perhaps been partly the cause of the readiness of botanists to class the glucoside which yields it, and hence the whole class of glucosides, among the products of excretion.

The localisation of the amygdalin is calculated to throw a good deal of light upon the question of its probable function and fate. For many years attention has been given to it, at first, owing to imperfect methods of research, without much practical result. Improvement in technique has, however, yielded very valuable results, and has led to conclusions greatly at variance with those held thirty years ago. Thomé (60), who wrote in 1865 upon the nutritive materials contained in the sweet and bitter almonds respectively, said that amygdalin occurs in the parenchyma of the cotyledons of both varieties, and that its corresponding enzyme, emulsin, is only present in the bitter almond, being localised in the weak fibrovascular bundles that are in the cotyledons. This statement has been shown to be the exact converse of the truth. Portes (61), who worked twelve years later, showed that the glucoside and the enzyme occupy different parts of the seed, the former being distributed in the cotyledonary parenchyma, while the latter is to be found in the axis of the embryo. Pfeffer (62), in his *Pflanzenphysiologie*, suggests that this localisation is not accurate, and that the two bodies probably occupy the same cells, the only degree of separation being that the ferment is in the protoplasm and the glucoside dissolved in the cell-sap. In 1887 Johansen (63) by chemical methods succeeded in ascertaining the distribution of the

two bodies in the seeds. He found the emulsin to be present in both varieties of the almond, and to be chiefly localised in the fibrovascular bundles. He further ascertained that the glucoside, *amygdalin*, is only present in the cotyledonary parenchyma of the bitter one. The absence of the glucoside from the seed of the sweet almond points, of course, to the conclusion that even if it be a nutritive body it is not one of very great prominence in the nutrition of the embryo on germination.

Guignard has published within the past few years a series of researches which deal primarily with the localisation of the enzymes which decompose the glucosides, but which incidentally throw a certain light upon the occurrence and meaning of the latter. In his first papers (64) he treats of the amygdalin which is found in the almond and in the cherry laurel, in the latter of which it is found to have a fairly copious distribution. He confirms Johansen as to its position in the seed of the almond, and still more closely localises the enzyme. In the laurel (*Prunus lauro-cerasus*) the parenchyma of the leaves as well as of the axis appears to contain it in solution in the cell-sap. The occurrence of the emulsin is confined to the neighbourhood of the conducting tissues, it being chiefly found in the endodermis round the fibrovascular bundles. In the bundles of the axis of the embryo in the almond the ferment occurs in the many layered pericycle, chiefly outside the bast. The distribution of the amygdalin is not definitely known. It may happen that the fluid sap containing it may travel along the cellular tissue, and the occurrence of the ferment which decomposes it, in the immediate neighbourhood of the conducting tissues, suggests that it is charged with the duty of preparing from the glucoside certain nutritive products that may easily make their way to the conducting tissues, and so travel to the actual seats of constructive metabolism. That sugar so travels is of course a matter of every-day experience, but whether or no the remaining products are made use of in a similar way is open to discussion. On the other hand it may be that the amygdalin descends by the conducting tissue of the bast and undergoes decomposition as it passes downwards, yielding simpler products to the young cortex.

In the face of the problem of the utilisation of the bodies resulting from the action of emulsin upon amygdalin great importance must be ascribed to the recent work published by Treub on the occurrence and meaning of hydrocyanic acid in the tissues of *Pangium edule* (65), one of the Bixaceæ. This compound, according to the author, does not occur as a glucoside, but in the free condition, and is present in relatively large amount. Greshoff found more than 1 per cent. to be hydrocyanic acid of the dry weight of the plant in one sample among many others analysed. A brief *résumé* of the author's conclusions seems not to be out of place here, as throwing light upon the question of the nutritive value of the glucoside of the laurel. Indeed it seems not improbable that the hydrocyanic acid itself may be regarded as, in some cases at least, a reserve material.

Treub has made a careful investigation into the localisation of this principle in the plant, using as his method the reaction given in the formation of Prussian blue when hydrocyanic acid comes in contact with a ferric salt in the presence of hydrochloric acid. The reaction is very distinct and takes place well in the interior of the cells, causing those which contain the hydrocyanic acid to stand out with great distinctness.

In the whole of the adult axis, both stem, root and peduncles, he finds it to exist in quantity in the conducting tissue of the bast and pericycle. In the leaves it is still in the same regions, but is more widely spread, nearly all the parenchymatous tissue of the blade containing more or less of it. The epidermis especially is noteworthy, showing it present in the basal cells of the hairs which the leaves bear, and in certain idioblasts which contain also crystals of oxalate of lime. In the young fruits and those which are growing a considerable quantity is present, partly in the bast and partly in parenchyma outside the conducting tissue. In the seeds there is an accumulation in the peripheral layers of the endosperm and in other cells of the same tissue abutting on the embryo.

In these regions, and in the cortex, and sometimes the pith of the axis, Treub describes the hydrocyanic acid as

existing in special cells which are sharply marked off from the others round them when stained as above described. These special cells vary a good deal in number, apparently according to the amount of the acid present in the plant, and have no very specially regular distribution. Indeed it seems probable that any cell of the tissue may become a centre of deposition of the acid. Generally, if not quite isolated, they only occur two or three together. Certain of the fibres of the pericycle may be observed almost similarly isolated.

Treub further says that these special cells of the cortex or of the pith derive their supply of hydrocyanic acid from the conducting tissue of the bast and that the amount of them and consequently of the acid varies with the condition of the stem.

Tracing the hydrocyanic acid upwards through the axis by means of longitudinal sections it can be found to extend throughout its whole length, but to disappear at a little distance from the growing point, the apical meristem of which contains none.

It is impossible to avoid being struck with the similarity here exhibited to the fate of sugar, amides, etc., which as we have seen can be traced up to the seats of constructive metabolism and there cease, apparently giving rise to protoplasm. If this be so, the hydrocyanic acid must be regarded as a plastic material, unsuitable as at first sight it would appear for that purpose.

This view is supported by several observations which the author details at some length. He finds that in the apices of young shoots which have suffered an arrest of growth, there are more of the special cells containing the hydrocyanic acid than there are in similar ones which are undergoing rapid elongation. That is, where there is active consumption of plastic material there is no accumulation of the acid, but where plastic substances are compelled to remain unused, hydrocyanic acid is one of such stored bodies.

Another series of observations considerably strengthens this view, while it points more definitely to the ultimate purpose of the acid. In many of the special cells the latter

may be seen to be accompanied by quantities of proteid substance. Taking young cells near the apex of the shoot the special cells contain the hydrocyanic acid alone, showing that it precedes proteid in the time of its occurrence. A little farther back the proteid can be detected, and gradually as sections are taken at increasing distances from the apex it increases in amount while the acid diminishes. As the active life of the cells becomes less and less vigorous, the proteid becomes more and more preponderating in the cell contents, and ultimately cells are found which contain proteid only, the hydrocyanic acid having all disappeared. The same succession of events can be seen if the development of the pericyclic fibres be traced towards the apex of the stem.

There seems from these observations to be very strong reasons for supposing that hydrocyanic acid is a nutritive substance and leads at any rate in these plants to the formation of proteid.

Treub holds that this is its immediate function; he believes it to be primarily formed in the leaves, principally in the basal cells of the hairs and the idioblasts with calcic oxalate in the epidermis of the leaves. Thence it makes its way to the conducting tissues of the bast and pericycle and travels to the apical meristems. It is thus primarily a body originating only in the constructive processes, and not, as in the cases of the almond and cherry laurel, the product of a decomposition of a glucoside. Indeed Treub says very emphatically: "L'acide cyanhydrique du Pangium edule n'est *pas* un produit de decomposition ou de dèsassimilation," basing the statement on both indirect and direct arguments. The former are founded on the localisation of the product in the bast and pericycle and its evident transportation by the bast tissue. The latter involve the consideration of its localisation with a material which serves as a temporary proteid reserve in the same elements of the tissues, and the order of appearance and disappearance of the two substances in such special cells.

That hydrocyanic acid can subserve not only the formation of temporary reserves of proteid but can be used,

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immediately after its first formation, by the leaves in which it is formed also appears certain. When plants whose leaves contain it are put for some days in the dark the acid gradually disappears, and as usual in such cases their whole metabolism suffers. On being again illuminated the vital processes gradually resume their activity. If a plant be put in the dark till nearly all the acid has gone from the leaves and then it be brought into the light, the little that remains is soon removed by the returning activity of the metabolism.

That the acid is used, and not simply transported from the leaves, can be shown in another way, by cutting a circular section through the conducting tissue of the petioles, when removal by transport becomes impossible. Yet the hydrocyanic acid disappears gradually.

It was said above that in some cases the hydrocyanic acid itself might be looked upon as a reserve material. This seems to be the case in the special cells described by Treub in the cortex of plants when they do not contain also proteid. In such cases we seem to have temporary reservoirs to supply local and transitory needs and to supplement the current passing along the bast. "Dans les endroits non on pas suffisamment desservir pour le systême conducteur libérien ces usines locales prennent naissance, et en plus grand nombre, à mesure que la plante a on aura besoin dans ces endroits de plus de substances plastiques." Thus in the older part of the stem, where the active life is confined almost altogether to the cortex, the latter contains many of these special cells, while they are absent from the rest of the fundamental tissue. Where they are present, as in certain portions of the petioles, active life continues, although it may be decadent in other parts.

This temporary storage comes out very prominently in the cases of the developing fruit and seed. At the base of the former, just above its point of junction with the pedicel, there is a very marked accumulation of the hydrocyanic acid, the cells staining blue under the treatment described being much more numerous than lower down the stalk. The

peripheral layer of the seed in its young condition is also supplied very fully with these local reservoirs. We appear to have here a deposit laid down to supplement the regular stream which is passing all about the plant by means of the conducting tissue of the bast. It is doubtless derived from the circulating supply, for if the latter be interrupted by a section passing across the stem through its path, the disappearance of the acid takes place from the bast tissues below the wound some time before it does from the isolated special cells of the cortex.

From the work of Treub and of Guignard then it seems increasingly probable that the glucosides are reserve materials, and not simply bye-products or products of excretion. Nor is it apparently only the sugar in them which has a nutritive value, but the other products of their decomposition have a particular part to play in the metabolism. This is certainly the case with hydrocyanic acid, and no doubt further investigation will show that it is the same with other products similarly formed.

Guignard (66, 67) has made similar researches to those already described upon the plants of the natural orders Cruciferæ, Capparidaceæ, Tropœolaceæ, Limnanthaceæ, Resedaceæ and Papayaceæ; which all contain the ferment *myrosin*, a body capable of decomposing more than one glucoside. There are several of the latter compounds found in this group of plants, the best known of which are sinigrine, and sinalbine. Sinigrine is found in the black mustard (*Brassica nigra*), and is often called myronate of potassium. On decomposition it yields besides sugar a volatile body, sulphocyanate of Allyl, and potassic hydrogen sulphate. Sinalbine, as its name implies, is found in the white mustard (*Sinapis* or *Brassica alba*). When decomposed the volatile constituent is found to be sulphocyanate of orthoxybenzyl. Others, the composition of which is not yet fully known, are those of the watercress (*Nasturtium officinale*) which yields phenyl propionic nitrile, the common cress (*Lepidium sativum*) affording the nitrile of alphatoluic or phenylacetic acid. Though the fate of these complex volatile bodies has not been investigated, it is

noteworthy that some of them at any rate contain cyanogen compounds, which may well be utilised after the manner of hydrocyanic acid itself as established by Treub.

Their distribution in the plants appears to follow that of the amygdalin in the Rosaceous group, but very little definitely is known on this head. The enzyme which splits them up is according to Guignard always found in special cells which do not contain the glucoside.

Very closely allied to the group of the glucosides is that of the tannins, about the importance of which there has been a good deal of controversy. Some of them are no doubt glucosides, yielding among their products of decomposition gallic acid and sugar. Others are apparently not so associated with a carbohydrate group. They are very widely distributed, and often occur not only in parts of plants which are devoted to storage of materials, but in the tissues where active metabolic work is going on. The task of deciding whether or no they serve as reserve materials or as bye-products is consequently not easy.

The two views have been strenuously supported by different writers. Sachs, while working on the germination of the Scarlet-runner (68) in which tannin is comparatively plentiful, suggests an antithesis between carbohydrates and proteids on the one hand, and the tannins and colouring matters on the other, the latter being in his opinion only bye-products. He advances in support of his view the fact that they appear or increase with renewed growth of the embryo, instead of diminishing as reserve materials should do. Their appearance is coincident with the chemical changes in the undoubted reserves which lead to the utilisation of the latter. The same view is advanced by Schell (69), who suggests that in some cases, however, it may be a nutritive product. In the germination of certain oily seeds, chiefly of plants belonging to the Boroginaceæ, tannin, which is present in addition to the oil, diminishes in quantity during the germination. In the stem of the mature plant there is during the winter a considerable quantity of tannin which almost vanishes as spring advances. On the other hand he finds in certain almost parallel cases that the tannin accumulates instead of diminishing.

The view that these bodies have a nutritive value has been supported with some emphasis by other writers. Wigand associated it very closely with the carbohydrates, and thought it was an essential factor in vegetable metabolism. Wiesner also supported the view of its carbohydrate relationships, and indicated a probability that it stands between the starch and cellulose groups and the great class of resins, etc. The latter relationship has been again brought forward by Hillhouse (70), who found in *Pinus sylvestris* that as resin increases in the stem tannin diminishes in like proportion, and that the cells surrounding the resin ducts invariably show its presence. Hartig suggests that tannin remains in the oak through the winter in the form of grains similar to starch grains, but distinguishable from the latter by characteristic reactions. These grains, he says, are dissolved and utilised in the spring. In his later writings Sachs inclines to the same view; he says that besides those which must be looked upon as excreta or bye-products, some of the tannins of the oak are most likely to be regarded as reserve products, on account of their origin and disappearance and their behaviour generally during the growth of the plant (71).

The localisation of tannin in the different parts of the plant does not give us much assistance in determining which of these views has most to support it. It is often found in special sacs in the midst of metabolic tissues; it is very frequently found in epidermal cells, either in the interior or saturating the cell wall; it is extremely prominent in bark. These positions certainly suggest that it is of but little value as a food-stuff; on the other hand it is often abundant in assimilating parenchyma in which starch formation is proceeding.

In Hillhouse's paper (70) already alluded to, the author describes a considerable number of observations he made to determine whether or no a disappearance or diminution of tannin could be detected in the spring, and if so, whether it was a reasonable conclusion that such diminution indicated a utilisation of the vanished portion.

He investigated a large number of trees in which tannin

is present in greater or less amount, and noted the changes in the amount present in winter and in spring in their various tissues. He concludes that in no case is there noticeable a diminution of tannin in early winter as starch accumulates, and there is no sign that the starch is formed at the expense of the tannin. When growth recommences in the spring, instead of tannin disappearing from the older tissues it makes its appearance in quantity depending on the amount of growth. The tissues of the bud are commonly crowded with it. Hillhouse's experiments proceeded upon three lines. In the first place plants or parts of plants rich in tannin were made to grow under conditions in which assimilation of CO_2 was impossible; a second set of experiments consisted of germinating in darkness seeds containing tannin; and finally corms were investigated to see whether, as their nutritive material was transported to the newly-formed corm springing from them, tannin was transferred together with the starch.

In no case was any diminution or transference found, except in the case of *Pinus sylvestris* already alluded to, when the probability of the tannin being an antecedent of the resin became evident.

Those tannins which are undoubtedly glucosides must, however, be of some nutritive value, as they give off sugar on decomposition taking place. There is some evidence to show that during the ripening of certain fruits part of the sweetness is derived from an astringent principle resembling and probably identical with tannin, which diminishes in quantity as the fruit matures (72).

A similar uncertainty as to its physiological meaning must for the present be associated with phloroglucin and the compounds into which it enters, which are to be regarded as ethers corresponding to glucosides. There are two classes of these compounds, which have been described as phoroglucides and phloroglucosides respectively. The former include such bodies as hespentine, phloretine, etc., while the latter, which contain a sugar group in their formula, embrace aurantine, rhamnine, hesperidine, etc. They are somewhat difficult to localise, as the reactions they give

are either not well ascertained or not particularly distinctive. The most reliable is perhaps that with vanilin in the presence of hydrochloric acid. When this is made to react upon a cell which contains phloroglucin in the sap, the latter forms a fine precipitate of red granules which are composed of a compound of vanilin and phloroglucin, known as *phloroglucivanilin.*

Phloroglucin appears to be often present in the plasma of meristem cells rather than in the vacuole, for when chloride of vanilin is added to a tissue containing it the colouring mainly affects the protoplasm, some of the vacuoles remaining altogether uncoloured.

The distribution of phloroglucin, like that of tannin, leaves a good deal of uncertainty as to its physiological meaning. It has been investigated in recent years by Waage (73), who has carefully examined representative plants taken from almost all sections of the vegetable kingdom. Out of 185 plants submitted to experiment 135 showed it to be present, but in very different quantities. Of the 135, 51 contained a very considerable quantity, 41 less but still a tolerably large amount, while in 43 though present only a feeble reaction could be obtained. Its distribution was to a certain extent regular, for the author states that if one species contains it, it is found with tolerable certainty in all the species of that genus. The plants of the Polypetalæ as a rule show most, while the Gamopetalæ and the Monocotyledons are on the whole poor in it; lower down in the scale the Vascular Cryptogams and the Gymnosperms are charged with it to a degree intermediate between the other groups.

Examining the tissues of such plants as contain a considerable quantity it may be found in meristems and in permanent tissues. In axial organs it occurs in the epidermis and later in the bark; also in the parenchyma of the cortex, and in the sclerenchyma of the tissues more deeply seated. It is found sometimes in the endodermis; also in the dead cell walls of the xylem parenchyma, fibres, and vessels. The medullary rays frequently contain a certain quantity. It is uniformly absent from the bast

fibres and the sieve tubes, and may be present or not in the pith. When the epidermis contains it, it is usually in the hairs if any are present; even root-hairs giving evidence of a certain amount. Taking the members of the axis, Waage found that roots as a rule contain more than stems, unless the latter be rhizomes, in which it is fairly abundant. Petioles and the peduncles of flowers contain less than branches. In plants where the axis is highly charged with it, there is generally a quantity also recognisable in the leaves, chiefly occurring there at the edges near the endings of the veins, and further in the neighbourhood of the vessels of the latter. The palisade tissue of the leaf has usually more than the spongy mesophyll, and the upper has more than the lower epidermis. The seed as a rule contains but little, and that is only in the integuments.

If the disposition may be taken as any indication of its being a reserve material at all, the probability is that its value in the latter sense is but slight. The disposition of varying amounts in the medullary rays and its frequent presence in the cells of the cambium layer point possibly to its supplying nutritive material for the latter. On the other hand, its consistent absence from all parts of the seed except the integuments seems to indicate that storage of nutriment is not its main purpose. It may be that its value to the meristem tissues is based upon its easily oxidisable character, affording energy thereby, rather than being a reserve substance. Its occurrence in the leaves in the localities named suggests a formation in the mesophyll and a subsequent transport to the axial regions. But against the view of its value in metabolism as a reserve material we have the statement that light does not affect its formation. It is in Waage's opinion found in the cell-sap as a general rule, rather than in either protoplasm or choroplastids. It seems on the whole to be a product of destructive metabolism, for it occurs in the same cells as starch and sugar and may be derived from the latter by abstraction of three molecules of water, $C_6H_{12}O_6 - 3\,H_2O = C_6H_6O_3$. It seems to resemble tannin in that it often

increases with the greater development of the plant, and in being frequently plentiful in parts that are thrown off from the latter, such as old leaves, the coats of fruits, seeds, etc., and in regions withdrawn from active metabolism, such as bark and to a less degree epidermis. In a further paper Waage and Nickel suggest that it may possibly be a source of tannin, as the latter is generally found in the same parts as phloroglucin (74). Tannin does not appear, however, to give rise to phloroglucin.

Like tannin, therefore, phloroglucin appears to be on the whole an accessory product and only rarely to act as a reserve material. The compounds of it which contain sugar, *i.e.*, the phloroglucosides, may serve as such, yielding sugar on their decomposition.

In certain cases the alkaloids appear to serve as reserve materials, though their value in this direction is probably but slight. Many seeds which contain them in some considerable quantity lose them during germination, and other bodies, principally amides, replace them in the developing embryo or young seedling. This is especially the case with the seed of *Lathyrus Sativus*, an Indian species which contains sometimes as much as ·5 per cent. of its dry weight of an alkaloidal product known as *viciine* (75).

The possibility of alkaloids helping in such cases to form albuminoid materials or proteids has been pointed out by Jorissen (76) in his discussion of the chemical processes incident to germination, in which he claims for them a certain value as reserve materials. Heckel (77) comes to the same conclusion. He carried out experiments with *Sterculia acuminata*, *Strychnos Nux-vomica*, *Physostigma venenosum*, and *Datura Stramonium*, and found in all these cases that during germination the greater part of their alkaloidal principles disappears. He claims that this disappearance is due to a transformation into assimilable substances under the influence of the embryo. If the latter be extracted from the seeds, and they be then surrounded by or buried in moist earth, the alkaloids remain for a considerable time unchanged.

The conclusions of Jorissen and Heckel are disputed by

Clautriau (78), who finds another explanation of the disappearance of the alkaloids during germination in a possible destruction of them as deleterious bodies which would affect prejudicially the development of the young seedling. He has ascertained with considerable precision the distribution of the alkaloid in the seeds of *Atropa Belladona*, *Datura Stramonium*, and *Hyoscyamus Niger*, and states that it is confined entirely to a layer of cells situated between the albumen and the integument of the seed, which when the latter is mature is very much reduced in its dimensions. This layer is much more prominent while the seed is ripening, consisting of many cells with very rich contents, the latter consisting of starch and albuminoid substances as well as alkaloids. As the albumen grows, this nourishing layer gradually yields up both starch and proteids, while the alkaloid persists; the cells become gradually nearly empty, and dry up considerably, ultimately becoming dead. In this condition they still contain the alkaloid, the quantity of which does not diminish during the changes described. When the seed is mature, this layer is very thin, the cells being flattened and compressed together, forming a sort of membrane in which the alkaloids remain, partially or wholly combined with an organic acid.

The nutritive value of the alkaloid seems improbable when we consider the disappearance from this layer of the starch and proteids, and the retention of the former. If it were then a reserve product it would in all probability accompany the other undoubted nutritive bodies. Clautriau has obtained further information on this point by depriving seeds of *Datura Stramonium* of this alkaloidal layer and submitting them to germination, either in moist earth or in an atmosphere saturated with watery vapour. He found that under such conditions they germinated normally, and produced young seedlings which differed in no particulars from normal seedlings of *Datura*.

Clautriau extended his researches to other plants than those named, particularly *Conium maculatum*, from which he obtained the same results.

Examining the young seedlings grown under these

conditions, no alkaloid being allowed to remain in the seed, Clautriau found that the active principle made its appearance in considerable quantity, and chiefly in the growing apices. The same thing was noticeable in the development of morphine in the poppy (79), where a more gradual formation was detected. Morphine does not show itself at the outset of the development of the plant, but appears to be preceded by another alkaloid, giving very clear reactions, which does not seem to be identical with any of the nitrogenous principles extracted from opium.

The conclusion that must be drawn from these investigations is that these alkaloids, and hence probably all such bodies, are not to be regarded as reserve materials, but as bye-products or excreta, appearing coincidently with the active metabolic processes of the growing plant.

Besides these accumulations of more or less complex organic compounds in the tissues of plants we meet with certain cases where inorganic material is deposited with a view to subsequent utilisation. These are, however, of much less importance and only occur in comparatively few plants. We have the well-known globoids in the aleurone grains of the castor-oil seeds, the seeds of *Bertholletia excelsa* and several others. From their disposition and fate, and from the fact that they afford a supply of phosphorus, it is probable that we may include them in this group. In certain cases also the collections of crystals of calcium oxalate gradually disappear from the cells in which they are deposited, and so seem to minister to the needs of the plant for calcium, an element whose function, however, is still practically unknown.

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AFRICAN GRASS FIRES AND THEIR EFFECTS.

MANY parts of the interior of tropical Africa consist of wide grassy plains, occasionally varied by scattered trees, but usually very bare and monotonous in appearance. In the rainy season these steppes are green with vigorously growing grass, and patrolled by hundreds of antelopes and other kinds of game; a few months afterwards when the rains are over, they are covered by blackened ashes and charcoal, and not a living creature will be visible except perhaps a few birds or a very occasional ground-rat.

These fires are usually due to the natives, who find that the bush can be most easily cleared by their assistance, though they are often lighted to satisfy the childish delight in a big blaze which is characteristic of the Suahili porter.

Their effects are most interesting, both economically and also in the way in which they entirely change the aspect of the vegetation.

It is, of course, immediately obvious that all the valuable feeding material of many square miles of luxuriant grass is by these fires entirely wasted; but, besides this, the soil is never permitted to grow rich through the accumulation of leaf-mould and stems, and in fact the land is every year brought back into exactly the same condition. No true turf is formed, and the soil remains more like the subsoil in cultivated countries and never becomes in the least improved.

The effect on the vegetation is very curious. The season of flowering for many trees and herbaceous plants is completely altered. A large number of low-growing herbaceous plants possess woody root-stocks or some sort of underground store of nourishment. With the very first shower of the rainy season, these stores send up flowering stems entirely without leaves, and the bare and blackened earth is studded with the bright purple flowers of

Dolichos spp., the blue *Pentanisia Schweinfurthii*, little white Euphorbias, *Lasiosiphon* spp., etc. These all have the appearance of a flower cut off and planted in the earth, and give rise to remarks on the collector's carelessness in not bringing leaves when worked up by untravelled botanists. With the setting in of the rains, the stems begin to grow and produce leaves until, when the grass has sprung up, all these herbs are in full foliage. This habit is of great advantage to the flowers concerned, as insects can readily perceive the scattered flowers which in the grass would be quite inconspicuous. The same thing occurs in many of the trees. Several species of *Dombeya*, for example, send out their flowers at this foreshadowing of the rains and are most conspicuous.

Another curious effect of the fires is the manner in which trees are either kept down or obliged to protect themselves in some way against their action. In the more arid plains trees seldom exist, or if present occur in the form of stumps perhaps ten years old, but never able to grow higher than a foot or so. Such stumps put out every wet season vigorous shoots, which are annually burnt away and only the short stem with another layer of wood is left to survive.

Of the trees which do manage to exist in spite of the annual conflagration, the most remarkable are the tree Euphorbias, often twenty to twenty-five feet high. These have angular fleshy branches protected by a leathery epidermis, and besides their milky juice, which contains gum, caoutchouc and other substances, have a large amount of mucilage or slimy matter in the ordinary tissue. This latter is a strongly waterholding substance, and the most violent fire seems unable to do more than scorch a very few of the outermost branches.

It is a most curious fact that though when living they resist fires in this wonderful manner, dead branches make an excellent fire and blaze up most vigorously. I cannot understand this difference.

Of the other trees which continue to thrive in these places, there are some seven species which grow in abun-

dance; there will be usually 500 of one of these species to every individual of some other kind. I brought home specimens of the bark of these six or seven forms, which were given to Professor Bretland Farmer for examination, who replied as follows: "I examined your specimens of bark and they all agree in possessing cells which show a certain amount of gummy degeneration of the cells in the bark, together with the presence of a considerable amount of sclerotic cells; it seems not impossible that these two facts may be connected with the resistance of the plants to the fires, and I found as a matter of fact that, on comparing the rate of burning of these barks with that of laburnum, they were very slowly consumed.

"I should have added that there are repeated periderms, and intermixed with the cork are the sclerotic cells already mentioned." Now the artificially produced cork of commerce shows great similarity in some respects to the cork of these fireproof trees. The process adopted both with the birch and the cork oak is to carefully peel off the cracked superficial layer of bark or "male cork" (this is known as "démasclage"). After this the layer of cork increases enormously and may perhaps attain to 17 cm. in thickness if left untouched: the result is the ordinary commercial article. I do not think that it is going too far to say that we have in grass fires a natural "démasclage" process, for they will certainly destroy the outer more or less dead tissues.

From the researches of Henslow,[1] Tschirch[2] and Volkens[3] on desert plants, it may be considered proved that cutin, which most modern authorities consider nearly identical with suberin, is directly increased by dry and arid conditions, so that this direct effect is probably also of use in increasing the deposition of corky matter. Both evils—the fire and the drought—have, as so often happens, brought about their own remedy. The sclerotic cells (or stone cork?) may doubtfully be set down to the same cause, for

[1] *Origin of Plant Structures.*
[2] *Angewandte Anatomie* and *Linnea*, 1881.
[3] *Flora der egypt. arab. Wuste.*

culture experiments (Duchartre and Henslow, *loc. cit.*, p. 57) show that sclerenchyma may be directly diminished by a more moist atmosphere.

The occurrence of gum is not so clearly dependent on the climatic conditions ; its use in these forms is, however, obvious enough, for all apertures by which water might be lost are, so to speak, gummed up. This is quite similar in physiological action to the drops of mucilage or gum which hermetically seal the vessels exposed by cutting across a branch of any ordinary deciduous tree.

It is true that the production of gum is known to be most abundant in a dry and hot season, but according to the explanation given by Tschirch, *loc. cit.*, p. 211 (and an identical account has been given me by Mr. Malcolm Dunn as the result of experience), this is due to the gum being squeezed out by the contraction of the bark following on a wet period, during which the masses of gum in the bark are greatly swollen. I cannot find any explanation of the actual cause of the change of cellulose into gum, but Mr. Malcolm Dunn states the general opinion that it is abundant after a severe shaking of the trees, as, for example, in a violent wind. Such places as those here treated of are certainly exposed to wind (otherwise they would be covered by forest, according, that is, to my experience), and it is possible that the wind may have assisted in starting gum formation ; but if, as is not unlikely, the wind acts indirectly by straining the layers of the cell walls, it seems more probable that the fierce heat of the fire, causing sudden and violent shrinking and warping of the bark, strains the cell walls in the same manner. This may of course be quite unproved, but the facts are sufficiently interesting to justify further research.

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